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TULANE STUDIES IN ZOOLOGY AND BOTANY

VOLUME 20
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A NEW SPECIES OF *EURYCERCUS* (CLADOCERA, CHYDORIDAE) FROM THE SOUTHERN UNITED STATES[1]

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ABSTRACT

Two species of *Eurycercus* occur in the southern United States, of which *E. microdontus* in the subgenus *Eurycercus* is described here. Its outstanding characteristic is that the large number of minute teeth on the postabdomen exhibits a sigmoid relationship to size of animal, rather than linear as in the other known species. Moreover, although the two major populations from North Carolina and Florida agree very closely in most morphological details, they differ significantly in this regression and in the body size at which reproduction begins. The meaning of these differences in terms of evolution within the genus is not yet understood. Other characters that are size-dependent, particularly details of setation and spinulation on trunk limbs I and II, are described by regressions and compared with the other species. Relatively little can be deduced concerning the biology of the species because of the small size samples available.

INTRODUCTION

Two species of the highly distinctive genus *Eurycercus* occur in the south and southeastern region of the United States and south at least to Mexico City. Neither is the species *E. lamellatus,* which is the only one presently reported as occurring in the United States, excluding Alaska (Brooks 1959). Until recently (Frey 1971) *E. lamellatus* was considered to be widespread over North America and Eurasia, with disjunct populations in Argentina and South Africa. Now (Frey 1973, 1974) this taxon is known to be made up of a number of species, each with a much more restricted distribution. *E. lamellatus* sensu strictu is the dominant, and probably in most water bodies the only, species in Western Europe and for an unknown distance eastward through the northern half of Asia. Evidence to date suggests it does not occur in North America at all.

The most outstanding characteristics of the nominate subgenus to which *E. lamellatus* sensu strictu belongs are a sharp keel on the shell in all instars and a pronounced transverse fold or notch immediately behind the median head pore (Frey 1974). Moreover, the keel actually begins on the head shield behind the median pore, which results in a triangular posterior extension of the head shield where it contacts the keel on the shell. The original paper on head shields and head pores of the chydorid Cladocera (Frey 1959) contains a sketch of a *Eurycerus* head shield from White Lake, N. C., having the same triangular extension posteriorly as in the European taxon and hence at that time judged to be the same. This was an unfortunate coincidence that may have delayed the recognition of the plurality of *Eurycercus* for some years, because from almost any other region of North America, particularly from the more northern lake districts in the

[1] Contribution No. 982, Department of Zoology, Indiana University.

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United States and Canada where *Eurycercus* is a common component of the littoral fauna, the head shields are rounded behind. Close examination of intact specimens of these populations would have revealed an unkeeled shell and the head pore located on a rounded protuberance – features that are characteristic of the subgenus *Bullatifrons* (Frey 1974) to which the second species in the South and Southeast belongs. Studies have not yet been made to determine if this latter species is the same as the widespread *Bullatifrons* sp. to the north, although superficially they seem different. Resolution of this matter will have to be delayed until the description of the northern taxon has been completed. Except for matters of distribution, the present paper is concerned only with *Eurycercus microdontus* sp. nov.

DISTRIBUTION

The region under consideration comprises the 11 states from North Carolina west to Oklahoma and south to Florida and the Gulf of Mexico plus Mexico. Here *Eurycercus,* although obviously widespread, is very sporadic in occurrence and seldom abundant, except perhaps in winter to late spring. The subgenus can be determined only from actual specimens. None of the literature records, including the lengthy description of Chien (1969), provides any basis for deciding the subgenus. Specimens derive chiefly from my own collections in North Carolina, Tennessee, Florida, Mississippi and Louisiana and from the sediment samples collected by DeCosta (1964). Scattered specimens were discovered in the U. S. National Museum and the E. A. Birge collection. Collections made in various states by R. V. Harmsworth, W. M. Lewis, Jr., P. R. Becker, Dewey Bunting, D. L. Dycus, D. C. Wade, and F. N. Young yielded occasional specimens or exuvial fragments. All known occurrences of the genus in this region are summarized in Tables 1 and 2 and Figure 1.

DeCosta (1964) found the remains of *Eurycercus* in the sediments of 7 out of 22 lakes sampled from Reelfoot Lake, Tennessee, to New Orleans, generally in very low abundance. Chien (1969) recovered *Eurycercus* from only 3 samples out of 80 collected along the entire length of the Pearl River in Mississippi and always in his lowest category of abundance. The only record from Texas is one intact specimen from Smithville in the E.A. Birge Collection. Intensive faunistic effort, documented by a number of master's theses from several universities in the State, have not disclosed any additional records (Becker and Sissom 1971).

For *Eurycercus microdontus* described in this paper (Table 1), the original material consisted of head shields and postabdomens from Pages Lake and White Lake in North Carolina, plus a few intact specimens and exuvial fragments from four lakes in Highlands Co., Florida, near the southern tip of the interior lake district. The Florida lakes were revisited in early December 1972 for the express purpose of obtaining more specimens and hopefully gamogenetic individuals. Intensive sampling yielded a total of only 70 specimens from Lake June in Winter, a few specimens each from two of the other lakes, and none at all from the fourth. No gamogenetic individuals were collected. More than 30 samples in the D. G. Frey Collection from various lakes in North Carolina, South Carolina, Georgia, Florida, Louisiana, Texas, and Mexico were searched for *Eurycercus* with completely negative results, except for an offshore sample of benthic algae from White Lake, N. C., which yielded the second largest collection of this taxon. The fairly extensive collection of D. L. Dycus from Georgia was not used in the morphological analysis because all specimens are badly distorted from preservation. Other records are based on scattered specimens and exuviae.

Fortunately, the raw sediment samples from all the lakes studied by DeCosta (1964) and from a few additional ones not used in his study have been stored in glass jars in a 5° room at Indiana University. Samples from his seven positive lakes in this region were processed, plus Sardis Reservoir, Miss., and Lake Charles, La., known to be positive on other evidence, plus three negative lakes that were significant to reexamine for one reason or another, and also Johnson's Lake, Tenn. Processing consisted of deflocculating 30-50

cc of raw sediment in 10% NaOH on a magnetic stirrer-hotplate (temperature kept below boiling) for about 1 1/2 hours. The sediment was then screened through a Clarke-Bumpus bucket provided with a No. 18 metal screen, which is fine enough to retain headshields and postabdomens of even the first-instar individuals of the two species of *Eurycercus*. Fractions of the residue were scanned systematically in a petri dish at a magnification of 15 X. Remains of *Eurycercus* were picked out as encountered and subsequently mounted in polyvinyl-lactophenol stained with lignin pink for study at higher magnifications. The results are given in Table 3.

Remains of *Eurycercus* were recovered from all of DeCosta's positive lakes, except Horseshoe Lake, La., from which he had recovered only a single fragment. Remains were also recovered from Sardis Reservoir and Lake Charles. All head shields, except three from Bennett's Bay in Lake Cocodrie, La., were from the subgenus *Bullatifrons*. The single *Bullatifrons* head shield from Lake Charles is interesting, because the specimen from this locality in the E. A. Birge collection is *E. microdontus*. Accordingly, another 50 cc of sediment was processed without disclosing any more remains of either species, demonstrating how very tenuous even some of the positive records can be. No remains of the genus were recovered from Alligator Lake and Lake Concordia in Louisiana, from the lagoon in Audubon Park, New Orleans, or from Johnson's Lake, Tenn.

A trip to some of the southern states was made in May 1974. *Bullatifrons* sp. was found at two of Chien's (1969) three *Eurycercus* stations in the Pearl River System, Miss., at Reelfoot Lake, Tenn., and at Courtebleau Bayou, La. (see Table 2). In addition, collections from various TVA reservoirs were examined at Muscle Shoals, Ala. No new populations of *E. microdontus* were discovered.

Aside from Lake Charles, which may be doubtful because of the 60 years between the records for the two species, both species

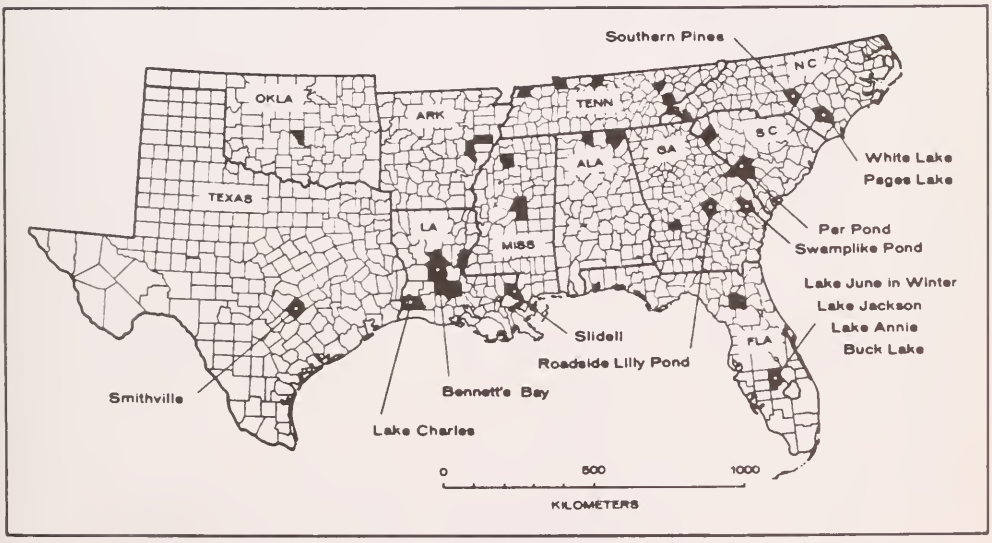


Figure 1. Known distribution by counties or parishes of the two species of *Eurycercus* in the southern and southeastern part of the United States. In addition there is a record from Mexico City (Juday 1915). Localities from which *E. microdontus* are known are indicated by a white dot and specifically labelled as to lake or locality. The other records are either for the species in the subgenus *Bullatifrons* or those for which the specific identification is uncertain (cf. Table 2). Most of the records from Tennessee and northern Alabama are from various T.V.A. reservoirs.

Table 1. Known occurrences of species of *Eurycercus (Eurycercus) microdontus* new species.

State	Locality	County or Parish	Date	Collection No.[1]	Number of specimens: Intact Specimens	Whole Exuviae	Head Shields	Post-abdomens	Shells
North Carolina	Pages Lake	Bladen	18-VIII-58	Sediments			21	16	3
			18-VIII-58	DGF 50			+		+
	White Lake	Bladen	27-VII-50	DGF 466	61		+		+
			19-VIII-48	DGF 468			++	+	++
	Golf Course Lake at Southern Pines	Moore	10-II-40	NMNH 81672	4				
South Carolina	Par Pond, SRP	Aiken	1-XI-73	DGF 3337			1		
			21-XI-73	DGF 3339	3				1
Georgia	Lilly Pond	Bulloch	20-IV-74	D.L. Dycus	29	3	3	1	3
	Marshlike Pond	Laurens	20-IV-74	D.L. Dycus	8		1	1	11
Florida	Lake Annie	Highlands	25-VII-60	DGF 111a			2		
			23-I-70	DGF 2918			5		4
			3-XII-72	DGF 2913-17	1	2	2		3
	Buck Lake	Highlands	9-VIII-60	DGF 173			1	1	2
			3-XII-72	DGF 2909-12	7		8		12
	Lake June in Winter	Highlands	3-VIII-60	DGF 144	9				
			3-XII-72	DGF 2905-08	70		7		13
	Lake Jackson	Highlands	12-VIII-60	DGF 181	9				2
Louisiana	Slidell	St. Tammany	31-XII-05	EAB tube Ey/1	5				
	Lake Charles	Calcasieu	27-X-03	EAB tube Ey/12	1				
	Bennett's Bay	Rapides	9-VI-60	DeCosta sediments			3		
Texas	Smithville	Bastrop	Oct. 1903	EAB slide C-55-17	1				

[1]DGF = D.G. Frey Collection in Bloomington; EAB = E.A. Birge Collection, also located in Bloomington; NMNH = National Museum of Natural History (=U.S. National Museum) in Washington, D.C. The samples from Par Pond were collected by W.M. Lewis, Jr., those from Pages Lake by Pamela Patterson. The D.L. Dycus samples from Georgia were provided by D.C. Wade. For Pages and White Lakes, + indicates present, ++ abundant.

occur together in Bennett's Bay and in Par Pond, S. C. In Par Pond only *Bullatifrons* was present – abundantly so – on 5 May 1973 and again on 30 January 1974 in much smaller numbers, and only *E. microdontus* (in very low abundance) in November 1973, suggesting a seasonal replacement of one species by the other. In other parts of the world where the ranges of two species of *Eurycercus* overlap, although any given body of water generally has only one of the species, both can occur in the same water body and at the same time. This is true, for example, of *E. lamellatus* sensu strictu and *E. glacialis* in Bislet Dam, Denmark (Kaiser 1959) and in Iceland (D. G. Frey observation in 1972) and of *E. lamellatus* and *E. pompholygodes* in several lakes in northern Sweden (Frey 1974) All two-species populations known to date involve species from different subgenera. At least in the lakes in Iceland and northern Sweden, both species of the pairs were present and reproductive at the same time, demonstrating that temporal displacement is not a requirement for occupying the same water body.

METHODS

Personal samples collected prior to 1965 were obtained with a short conical plankton net of 70 μm Nitex 15 cm in diameter mounted on a rod about 1 meter long. Subsequent samples were collected with a 110 μm mesh Nitex net of about the same size, which could be screwed into a sectional metal rod 3 meters long. The mouth of the latter net was protected by a hinged metal screen with meshes 5 mm bar measure to keep out leaves, macrophytes, and other coarse material. The entire contents were preserved in roughtly 5% commercial formalin.

In the laboratory subsamples were spread in a petri dish, systematically scanned at 15 X stereo magnification, and all specimens, exuviae, and exuvial fragments were removed as encountered, all of which were gradually transferred to glycerol for facilitating measuring and dissecting. Because of the small size of this species, all specimens were measured in temporary uncovered glycerol mounts with a Wild (M20) compound microscope using 10X eyepieces and either 3X, 10X, or 20X objectives, depending on the size of the specimen. By this procedure length of the specimen and length of the postabdomen and postabdominal claws could be measured conveniently, and the number of denticles on the postabdomen and of spinules on the postabdominal claw could be counted except in the smallest specimens. Details of the smaller exuvial components were studied in permanent mounts with 40X or 100X objectives.

In the previous studies (Frey 1973, 1974) the regressions of denticle counts on trunk limbs I and II as a function of length of the toothed zone of the postabdomen, which in turn is a function of overall size of the animal, were determined from complete exuviae recovered from the collections. In the present study virtually no intact exuviae were available, and hence these regressions had to be based on specimens sacrificed for dissection. Twelve specimens each from Lake June in Winter and White Lake, evenly distributed over the size ranges of the populations, except for the largest specimens which were too valuable for sacrifice, were used for this purpose. Dissections were made in glycerol at a magnification of 45X with a stereoscope, using tungsten needles. After removal of the head with its attached appendages and then the shell and postabdomen, the trunk limbs were separated longitudinally into right and left groups. In the smallest specimens only trunk limbs I and II were separated from their respective groups, whereas in larger specimens all trunk limbs were separated from one another. These were then mounted in polyvinyl lactophenol and eventually sealed with glyceel (available from ESBE, Toronto) for convenience in studying at whatever magnification was necessary, up to oil immersion.

All measurements and counts were punched on IBM cards for calculation of regression statistics and correlation coefficients, using the SPSS programs (Table 4). Although these simple techniques are not entirely appropriate because of the nature of the variables, they do identify which char-

Table 2. Known occurrences of the subgenus *Bullatifrons* of *Eurycercus* in the Southern United States and in Mexico. Where no specimens were available for examination, the subgenus could not be decided but it probably was *Bullatifrons*.

State	Locality	County or Parish	Date	Reference[1]	Comments	Subgenus
North Carolina	Highlands Lake	Macon	10-IV-65	DGF 1746, 2301	Very abundant (>1000)	*Bullatifrons*
	Santeetlah Lake	Graham	25-V-69	(Bunting)	1 parth. ♀, 1 ephip. ♀	*Bullatifrons*
South Carolina	Blackville	Barnwell	14-IV-65	DGF 2302	1 shell	*Bullatifrons*
	Par Pond, SRP	Aiken	5-V-73	DGF 3340-3343	Many specimens (>200) plus exuviae	*Bullatifrons*
			30-I-74	DGF 3344-3347	29 specimens plus >200 fragments	*Bullatifrons*
	Hartwell Lake	Anderson	9-I-71	(Bunting)	1 parth. ♀, 1 imm.	*Bullatifrons*
Georgia	Augusta region	Richmond	1907-1908	Turner (1910)	Abundant at 4-8°	?
	Flint River	Sumpter	22-V-69	(Bunting)	3 parth. ♀, 1 imm.	*Bullatifrons*
Florida	Newnan's Lake	Alachua	3-III-65	(Harmsworth)	1 imm.	*Bullatifrous?*
Alabama	Wheeler Res.	Limestone	2-IV-73	(Wade)	TVA: Trousdale Hollow	?
	Guntersville Res.	Jackson	13-VII-72	(Wade)	TVA: Slough above Sublet ferry	*Bullatifrons*
Mississippi	Pearl River System	Leake, Attala	10-V and 4-IV-67	Chien (1969)	3 sites; low abundance	?
			9-V-74	DGF 3413-3414	Chien's Sta. 3, 8; abundant at Sta. 3	*Bullatifrons*
	Sardis Res.	Panola	27-VIII-53	Hanebrink (1965)[2]	Only in Hurricane Bay; 48 specimens/liter	?
			7-VI-61	DeCosta sediments	2 head shields, 1 shell	*Bullatifrons*
			8-V-74	DGF 3412	1 specimen, 2 shells, 1 head shield	*Bullatifrons*
Louisiana	Horseshoe Lake	Concordia	June 1960 and 1961	DeCosta (1964)	65 exuvial fragments from sediments	*Bullatifrons* (See Table 3)
	Bennett's Bay	Rapides				
	Miller's Lake	Evangeline				
	Chicot Lake	Evangeline				
	Cazan's Lake	Evangeline				
	New Orleans Region		ca. 1905	Penn (1947)	Listed by Ed. Foster	?
	Kisatchie Natl. Forest	Grant	3-IV-72	(Becker)	2 specimens, 1 head shield	*Bullatifrons*
	Lake Charles	Calcasieu	4-IV-61	DeCosta sediments	1 head shield	*Bullatifrons*
	Courtebleau Bayou	St. Landry	10-V-74	DGF 3418	abundant: ephippial females and a few males	*Bullatifrons*

State	Locality	County or Paris	Date	References[1]	Comments	Subgenus
Tennessee	Reelfoot Lake	Obion	Early 1942	Hoff (1943)	In 3 of 214 collections	?
			4-VI-60	DeCosta (1964)	Remains from sediments	*Bullatifrons*
			11-VI-74	DGF 3426-3427	Lakeside Pond in Tenn. Natl. Wildlife Refuge: abundant; ephip. females	*Bullatifrons*
	Old Hickory Res.	Sumner	22-V-73 14-VI-73 11-II-74 4-IV-74 1-V-74	(Wade)	TVA: Gallatin Steam plant; river mile 240, 241	*Bullatifrons*
	Barkley Res.	Stewart	23-IV-74	(Wade)	TVA: river mile 104	?
	Nickajack Res.	Marion	12-XII-73	(Wade)	TVA: river mile 435	?
	Tellico Res. site	Blount	1-V-73	(Wade)	TVA: river mile 33	?
	Melton Hill Res.	Anderson	6-VIII-73	(Wade)	TVA: Bull Run Steam Plant	?
	Little Tennessee River	?	14-VI-73	(Wade)	TVA: 56 specimens	*Bullatifrons*
Arkansas	Horseshoe Lake	St. Francis	4-VI-60	DeCosta (1964)	4 remains from sediments	*Bullatifrons*
	5 mi. east of Clarendon	Monroe	30-III-59	DGF 511	Several specimens	*Bullatifrons*
Oklahoma	Entire state		Jan. 1947 – Sept. 1953	Jones (1958)[3]	Merely listed; no other information	?
Mexico	Mexico City		Feb. 1910?	Juday (1915)	Sunken Gardens and Lakeside Tivoli; no other information	?

[1]Samples DGF 2301, 2302, 3340-3343, and the specimen from Newnan's Lake, Fla., were collected by R. V. Harmsworth; Samples DGF 3344-3347 by W. M. Lewis, Jr.; Sample DGF 511 by F. N. Young; the sample from the Kisatchie National Forest, La., by P. R. Becker; and the samples from Santeetlah Lake, Hartwell Lake, S. C., and Flint River, Ga., by Dewey Bunting. D. C. Wade kindly made available his records and samples of *Eurycercus* from the TVA system of reservoirs. As specimens from most of these collections are no longer available, the subgenus cannot be decided for certain, although most likely it is *Bullatifrons*.

[2]Hanebrink (in correspondence) reported that the specimens have been lost. The taxon was collected only once.

[3]Jones reported in his paper that specimens of all taxa had been deposited in the National Museum of Natural History, but there is no record of these and hence no specimens.

[4]Since writing this paper I have been able to examine the PhD thesis of W.H. Jones from the University of Oklahoma, 1954: "Cladocera of Oklahoma." For the Chydoridae there are a disturbing number of discrepancies between Table I in the thesis and its abbreviated version in the published paper. The Thesis table indicates that Jones never collected *Eurycercus* in Oklahoma but that he *expected* it to occur. The published paper lists *Eurycercus* among the chydorids *known* to occur in Oklahoma, which is obviously incorrect.

Table 3. Reexamination of sediment samples from lakes along the lower Mississippi River collected by DeCosta (1964) in 1960 and 1961. All the head shields and shells (and hence presumably the other remains as well) were of *Eurycercus (Bullatifrons)* sp. except in Bennett's Bay, where 3 of 24 head shields were from *E. (Eurycercus) microdontus* (see Table 1).

	DeCosta's data			Remains recovered in present study			
No.	Lake and State	No. *Eurycercus*	% total chydorid remains	Head shields	Post-abdomens	Shells	Ephippia
24	Reelfoot Lake, Tenn.	4	1.9	19	6	1	
26	Horseshoe Lake, Ark.	4	1.0	46	14	11	
36	Horseshoe Lake, La.[1]	1	0.5				
37	Bennett's Bay, La.	3	1.2	24	4		
38	Miller's Lake, La.	25	6.6	47	46		2
39	Chicot Lake, La.	15	1.6	35	26	3	2
41	Cazan's Lake, La.	21	9.7	30	28	1	
——	Sardis Reservoir, Miss.	——	——	2		1	
——	Lake Charles, La.[1]	——	——	1			

[1]About 75 cc of sediment from Horseshoe Lake, La., and 100 cc from Lake Charles were processed. Hence, the taxon at these localities, if present, must be in extremely low abundance.

acters are size dependent, and they help to quantify differences between various species and populations. A product-moment correlation analysis of one set of data yielded no better insight than a simple regression analysis.

In an attempt to locate other specimens and records for this part of the continent, many individuals who had worked in this region were contacted by letter, mostly with negative results. Remains recovered from sediments may be one of the best ways of working out geographic distributions, once the species have been characterized sufficiently for their remains to be identified to species. Certainly DeCosta's (1964) sediment samples from the region of the Lower Mississippi River were invaluable in demonstrating that *Eurycercus microdontus* apparently has a smaller frequency of occurrence than *Bullatifrons* sp.

Eurycercus (Eurycercus) microdontus
new species

Type locality. Lake June in Winter, Highlands Co., Florida: approximate geographic coordinates 27.3°N and 81.4°W. The specimens were collected along the point of land close to U.S. Highway 27 at the northeast corner of the lake in SE 1/4, S25, T36S, R29E. This is where the species had been collected previously in 1960. At this locality the bottom drops off quite steeply, and the wave action can be strong. The specimens were collected chiefly around the emergent stems of cane at water depths up to 80 cm and up to 4 m offshore.

Type material. All 70 specimens collected on 3 December 1972 plus the scattered exuvial fragments recovered.

Holotype: A parthenogenetic female 1.67 mm long in alcohol has been deposited in the National Museum of Natural History, Washington, D. C., their catalog number USNM 1.51210.

Paratypes:

1. National Museum of Natural History: two reproductive females in alcohol and one mounted in glycerine jelly, catalog number USNM 151210.

2. British Museum (Nat. Hist.) London: three reproductive females, two in alcohol

(registration numbers 1974. 717-718) and one mounted in glycerine jelly (registration number 1974. 716).

3. All other specimens and exuvial fragments are in the D. G. Frey Collection in Bloomington.

Brief diagnosis. Small, seldom as large as 2 mm. Shell strongly and sharply keeled in all instars. Seen from the side, dorsal margin of head flattened or even slightly concave between compound eye and median pore. Rostrum short, not extending much beyond base of antennules. Many minute teeth on postabdomen, increasing to 140 or more in largest specimens. Anal groove broad and shallow. Middle seta on inner distal lobe of trunk limb I well developed, rather strongly and evenly curved, heavily chitinized.

Etymology. From Gr. *micro* small, and Gr. *odons, odontos* tooth. Named for the many extremely minute teeth on the postabdomen.

General comments: E. microdontus is the second described species in the subgenus *Eurycercus, E. lamellatus* sensu strictu being the first. These two species are readily separated from the other known species of the genus by the sharp dorsal keel in parthenogenetic females and males beginning immediately behind the median head pore and by the sharp notch behind the pore which interrupts the dorsal contour. Ephippial females of the subgenus *Bullatifrons* also have a keeled shell and hence might be confused with parthenogentic females of *E. microdontus,* but the keel does not involve the head. As a result the head shields even of these keeled ephippial females are rounded behind, rather than pointed as in the subgenus *Eurycercus.* Moreover, the keel of ephippial females is rounded, rather than sharp as in parthenogenetic females of the subgenus *Eurycercus,* as illustrated for *E. pompholygodes* in Frey (1974).

Although the populations from White Lake and Lake June in Winter are indistinguishable in most respects, they do differ significantly in number and shape of teeth on the postabdomen, in length of the postabdomen relative to body length, and in size at which reproduction begins. These differences and others will be pointed out where appropriate. At least for the present, the two populations are considered to belong to the same species.

Size. The sample from Lake June in Winter has a size range of 0.58-1.67 mm, with the smallest reproductive female (embryos in brood pouch) measuring 1.41 mm. The specimens from White Lake range in size from 0.58 to 1.61 mm, with individuals as small as 1.19 mm having embryos in the brood pouch. One isolated postabdomen 701 μm long from the sediments of Pages Lake corresponds to a body length of 2.02 mm, according to regression 1 in Table 4. The four specimens from Southern Pines, N. C., measured 1.75-2.23 mm, all larger than the largest specimens from Lake June in Winter and White Lake. Of the other miscellaneous specimens available, the largest was a parthenogenetic female about 1.7 mm long from Slidell, La. Hence, the species is small, seldom attaining a length as great as 2 mm.

Shape (Figs. 2-4). The shape of *E. microdontus* changes during ontogeny. The early pre-reproductive instars have the shell only weakly arched dorsally and the head relatively high (Fig. 4), resulting in an overall appearance rather similar to *E. macracanthus* although more elongate. Beginning immediately prior to maturity, the back becomes progressively more highly arched and more sharply keeled (Fig. 2), both characters being considerably more extreme than in *E. lamellatus.* The high arch to the shell can be regarded as one mechanism for increasing the brood pouch capacity and hence the reproductive potential of this small species.

In lateral contour the head is flattened or even slightly concave between the compound eye and the median pore (Figs. 2, 5). Because the rostrum is short, the compound eye is located closer to the tip of the rostrum than in *E. lamellatus,* more resembling *E. macracanthus* in this respect. The posterior margin of the shell slopes posteriorly resulting in the dorsal angle being located considerably farther forward than the ventral angle (Figs. 2, 4). This condition also tends to occur in *E. lamellatus* and *E. pompholygodes,* although not so extreme.

Table 4. Comparison of regression statistics for *E. microdontus* from Lake June in Winter (J), Florida, and White Lake (W), North Carolina. Regressions 14-19 are concerned with the denticles on scraping spines 2, 3, and 4 of trunk limb II, regressions 20-27 with the four clusters of spinules on the basal segment of the inner distal lobe of trunk limb I. All measurements are in microns, rounded off to the nearest 5 except for those made with the 40X and 100X objectives.

Variables					y			x					
Regression	Dependent (y)	Independent (x)	Locality	n	Range	Mean	Std. dev.	Range	Mean	Std. dev.	Slope	y–intercept	Correl. coeff.
1	length postabd.	length animal	W	58	205-545	349	82.5	585-1610	998	237.4	.3424	7.50	.98
2			J	68	210-660	389	124.8	585-1670	1029	306.3	.4060	−28.93	.99
3	length shell	length postabd.	W	12	590-1340	895	248.1	270-510	348	89.8	2.7396	−57.44	.99
4			J	8	540-1425	1010	313.1	225-610	429	135.5	2.3069	20.99	.99
5	length head	length postabd.	J	5	535-810	691	102.8	365-610	507	90.3	1.1373	113.92	.99
6	postabd. teeth	length postabd.	W	55	75-117	91.5	9.36	205-545	347	82.9	.0910	59.89	.80
7			J	71	83-146	108.2	20.42	215-660	386	121.1	.1563	47.91	.92
8	length claw	length postabd.	W	55	66-155	105.8	22.24	205-545	348	84.1	.2585	15.68	.97
9			J	34	71-178	130.5	29.49	225-660	477	118.8	.2434	14.49	.98
10	Claw denticles	length postabd.	W	35	26-39	32.8	4.12	205-545	370	88.9	.0425	17.09	.91
11			J	26	28-44	36.4	4.16	225-565	437	106.4	.0342	21.49	.87
12	claw denticles	length claw	W	35	26-39	32.8	4.12	66-155	111.3	22.67	.1672	14.19	.91
13			J	26	28-44	36.4	4.16	71-152	119.6	24.38	.1435	19.25	.84
14	SS2 denticles	length postabd.	W	21	12-22	18.1	2.99	270-510	352	84.5	.0308	7.30	.87
15			J	22	10-27	18.7	4.61	225-610	384	116.2	.0356	5.05	.89
16	SS3 denticles	length postabd.	W	23	13-24	18.9	3.14	270-510	343	86.8	.0330	7.56	.91
17			J	23	11-28	19.6	4.57	225-610	385	116.1	.0368	5.38	.93
18	SS4 denticles	length postabd.	W	21	15-25	19.3	3.39	270-510	340	90.3	.0225	11.64	.59
19			J	21	15-31	21.5	4.42	225-610	372	111.0	.0367	7.90	.92
20	prox. spinules	length postabd.	W	32	4-10	6.5	1.34	205-530	343	77.4	.0129	2.04	.74
21			J	27	4-11	7.0	2.17	225-610	406	121.6	.0157	.60	.87
22	dist. spinules	length postabd.	W	33	5-9	6.3	1.05	205-530	341	76.8	.0076	3.75	.55
23			J	27	4-8	5.6	1.15	225-610	394	125.8	.0076	2.62	.83
24	marg. spinules	length postabd.	W	22	3-11	6.7	2.21	210-510	335	80.6	.0231	−1.00	.84
25			J	25	1-11	5.6	2.58	225-610	403	132.4	.0173	−1.33	.88
26	basal spinules	length postabd.	W	17	2-14	7.1	3.58	270-455	347	63.4	.0488	−9.91	.86
27			J	14	3-14	9.1	3.34	300-610	459	108.2	.0233	−1.61	.75
28	head L/W ratio	head length	All	70	.97-1.18	1.031	.0484	410-1180	548	130.5	−.00019	1.15	.50

Head (Figs. 6-17). All appendages and the labrum were removed from head shields before mounting to get them to lie flat. This was also done for *E. pompholygodes* (Frey 1974) but not for the three species treated earlier (Frey 1973), which helps explain the seemingly greater variability in shape of these other three species. The convexity of the head shields varies considerably from one species to another, so that even with these precautions in preparation it is still difficult at times to get preparations satisfactory for characterizing the shape and for making length and width measurements. The relatively flat head shields of *E. microdontus, E. pompholygodes,* and *E. macracanthus* can be mounted with less distortion than the more convex head shields of the other two larger species.

The head shield is about as broad as long, the rostrum is short, not projecting much beyond the base of the antennules, and the transverse fold behind the median pore is much more deeply incised than in *E. lamellatus.* As a result, the median pore is visible with difficulty on mounted head shields, sometimes not being visible at all, at other times with only a small bit of the pore projecting anteriorly or posteriorly from the fold. The lateral pores occur at the ends of the transverse fold, which frequently obscures them and makes them difficult to see. The material at hand (or perhaps the species) was not suitable for working out size-dependent regressions of pore width and distance between lateral pores, as in *E. pompholygodes.*

The chitinous border of the free edge of the head shield is thickened somewhat anterior to the mandibular articulation, which seems to be characteristic of this species. The keel begins immediately behind the median pore, which results in a triangular extension of the head shield posteriorly, as in *E. lamellatus,* although more pronounced because of the higher and sharper keel. The ocellus is small, generally quadrate in appearance, and located near the anterior edge of the base of the antennules.

There are no obvious or consistent differences between the head shields of the Florida and North Carolina populations, or the three head shields from Bennett's Bay, La. A head shield of *Bullatifrons* from the latter locality (Fig. 18) has been included for comparison. Figure 19 demonstrates that there is a distinct tendency for the length/width ratio of the head shield to decrease in larger specimens, meaning that as the animals increase in size, the head shield becomes progressively broader relative to its length. Because no head shields from small Florida specimens were available, the White Lake and Florida populations could not be compared statistically, although the scattergram suggests no appreciable differences in the relationship.

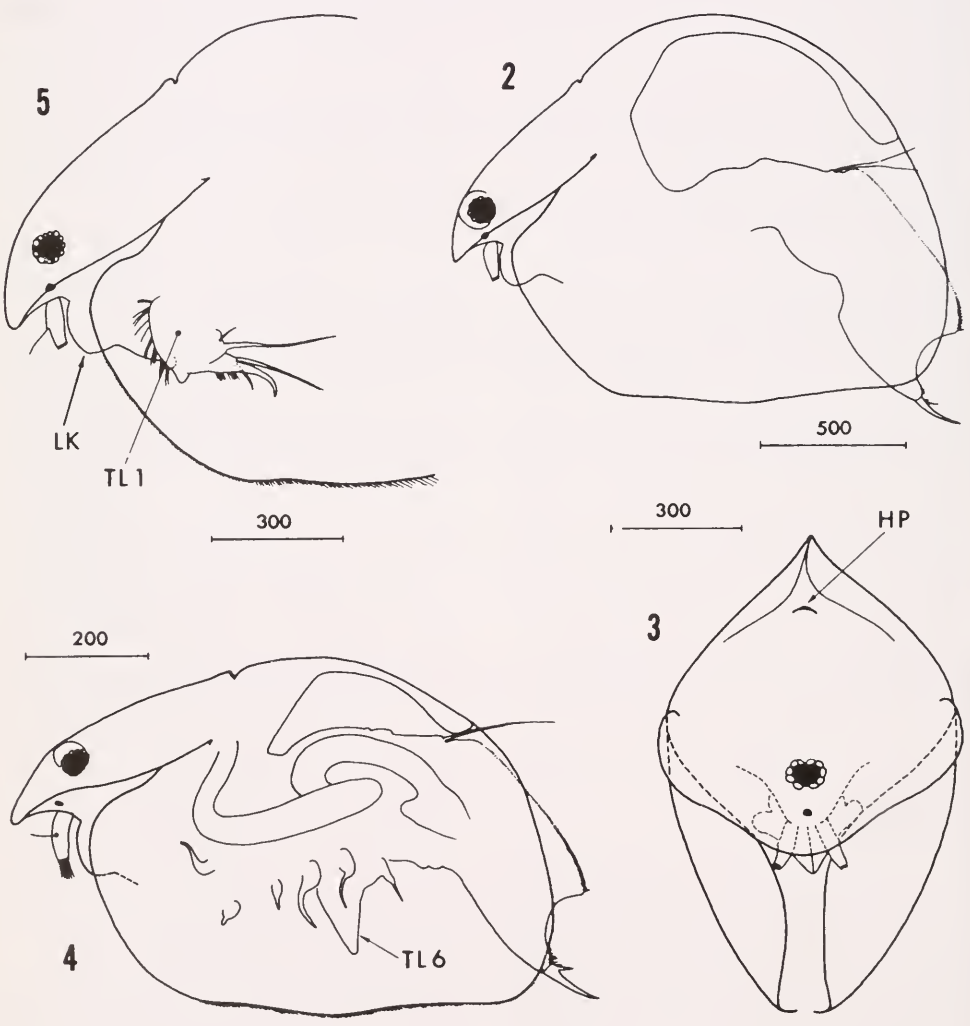
Labrum (Figs. 2-5). The labral keel is about intermediate in development between *E. pompholygodes* and *E. lamellatus,* not angled posteriorly as in *E. lamellatus.*

Antennule (Figs. 2-5, 30). The specimen drawn (Fig. 30) is good for general shape and proportions. The lateral seta arises from about the middle and is more than half as long as the antennule. The terminal setae could not be resolved in the specimen drawn, but in some other specimens there were definitely nine, subequal in length.

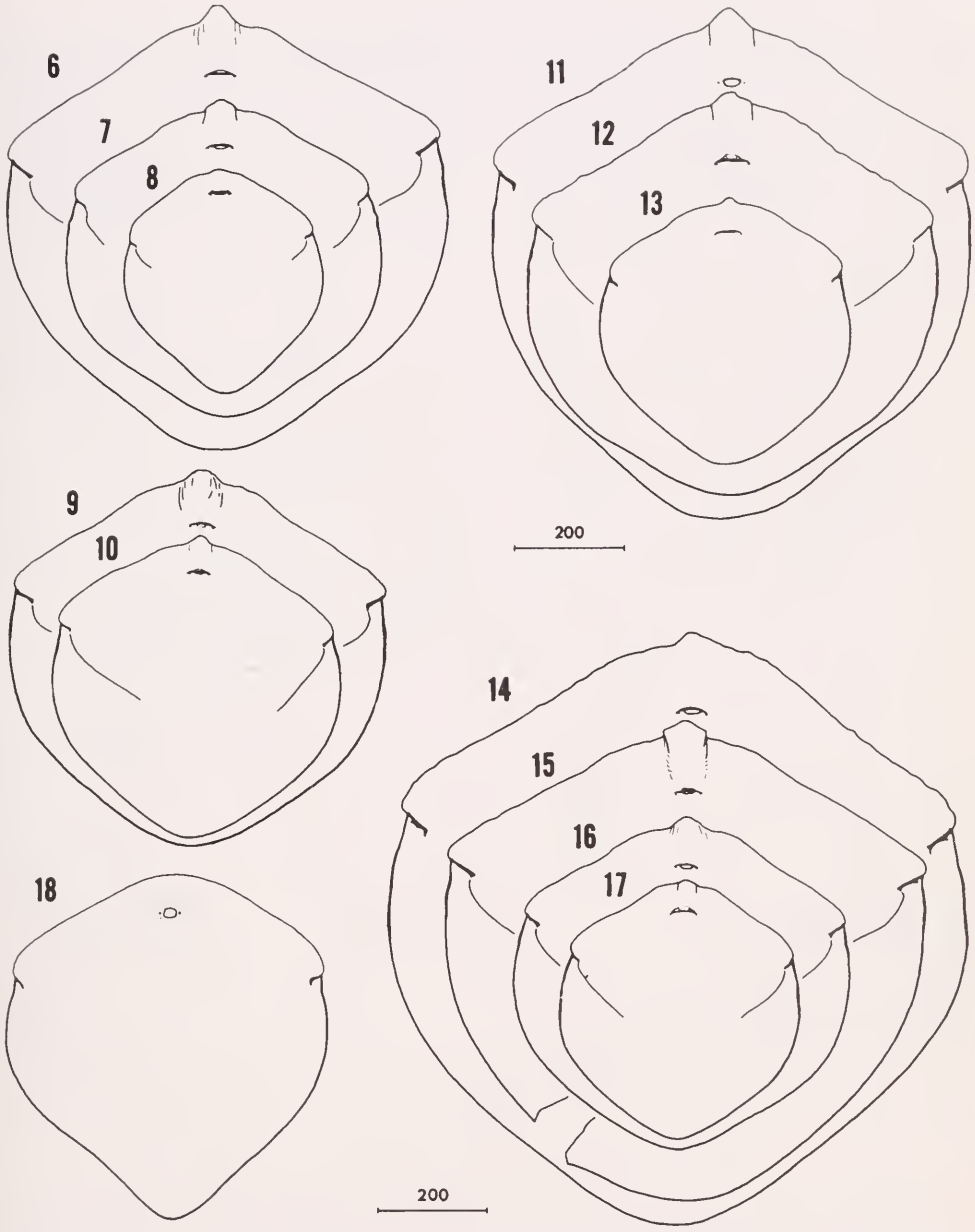
Antenna (Fig. 31). The antenna likewise seems relatively undifferentiated at the species level. It shares the common pattern of eight long and well developed swimming setae, three spines on the outer branch, and one on the inner branch (cf. Fig. 26 for *macracanthus* in Frey 1973). The various species may possibly be differentiated in the number and length of spinules on the rounded protuberance near the base of the antenna, or in the morphology of the two long 2-jointed setae nearby, but these characters have not yet been investigated.

Trunk limb I (Figs. 5, 20, 21). The morphology of trunk limb I is quite similar in all species studied to date (Frey 1973, 1974), the major differences at the species level occurring in the structure of the inner distal lobe (IDL). The three clasping hooks (Fryer's 1963 terminology) on this limb in *microdontus* are quite similar in shape and armament to those of *pompholygodes,* even though in a different subgenus, the chief dif-

ferences being 1) the setules on clasping hook 1 do not extend so far toward the tip, being more like *E. lamellatus* in this respect, and 2) clasping hook 2 is more strongly curved than in *E. pompholygodes* and much more strongly chitinized and hook-like than in *E. lamellatus*. As in *E. pompholygodes* and to a much less extent in *E. lamellatus*, clasping hook 2 seems to have a cutting edge distally (Fig. 21). Midway along this seta on its concave surface is a series of 6-8 setules that are quite discrete and can be made out quite clearly, with suggestions of other smaller setules distal to these. Only the tips



Figures 2-5. *Eurycercus microdontus* new species from the southern United States. 2. Parthenogenetic female, holotype, Samples 2905-2908 from Lake June in Winter, Fla. 3. Parthenogenetic female, Samples 2905-2908 from Lake June in Winter, Fla.: front view showing strongly keeled shell. HP, head pore. 4. Immature female, Sample 466 from White Lake, N. C.: note the single loop in the gut and the presence of a posterior intestinal caecum. TL6, trunk limb VI. 5. Parthenogenetic female, Samples 2905-2908 from Lake June in Winter, Fla.: enlarged view of front end showing the eye and ocellus, antennules, labral keel, and trunk limb I. LK, labral keel; TL1, trunk limb I.



Figures 6-18. *Eurycercus microdontus* new species (Figs. 6-17) from the southern United States. The head shields are mainly from detritus in the samples or from sediments. Only the few from exuviae could be related to length of postabdomen. The head appendages and labrum were removed before mounting to give the least possible distortion in shape. 6. Lake June in Winter, Fla., Samples 2905-2908. Length of postabdomen 610 μm. 7. White Lake, N. C., Sample 468. 8. Pages Lake, N. C., sediments. 9. Lake Annie, Fla., Samples 2913-2917. Length of postabdomen 515 μm. 10. Lake June in Winter, Fla., Samples 2905-2908. 11. Bennett's Bay, La., sediments. 12. White Lake, N. C., Sample 468. 13. White Lake, N. C., Sample 468. 14. Pages Lake, N. C., sediments. 15. Lake June in Winter, Fla., Samples 2905-2908. 16. Lake June in Winter, Fla., Samples 2905-2908. 17. White Lake, N. C., Sample 468. 18. *Eurycercus (Bullatifrons)* sp. from sediments of Bennett's Bay, La., to show the contrast in head shield morphology. This is the more common species in the region.

of the latter are apparent, their bases seeming to have fused together to form the proximal part of the cutting edge, as in *E. pompholygodes*. The two segments of clasping hook 2 are immovably fused together, as in all other species studied to date, and the basal segment of the hook seems to be immovably fused with the basal segment of the lobe. The latter condition is also true in *E. macracanthus* and *E. pompholygodes*, less certainly true in *E. lamellatus*, and possibly not true in *E. glacialis*. In all species clasping hooks 1 and 3 are articulated with the basal segment of the lobe, permitting movement relative to one another.

The basal segment bears the three clusters of spinules described in *E. pompholygodes* – designated proximal, distal, and marginal spinules – and in addition an irregular cluster of extremely small spinules – here designated basal spinules – lying in the general vicinity of the proximal spinules (Fig. 21). The number of spinules in each group increases significantly with size of specimen and all at about the same rate. Differences between slope and displacement of the regressions for the Florida and North Carolina populations are not significant, as the 95% confidence limits of the regressions overlap completely. More specimens are needed, and particularly at the upper end of the size distributions, to define these regressions more precisely. Certainly the proximal and distal clusters are more suitable for characterizing the species, the other two groups exhibiting greater variances and much broader confidence intervals. The rate of increase in each group (except basal, which was not studied) is greater in *E. microdontus* than in *E. pompholygodes*. Regressions have

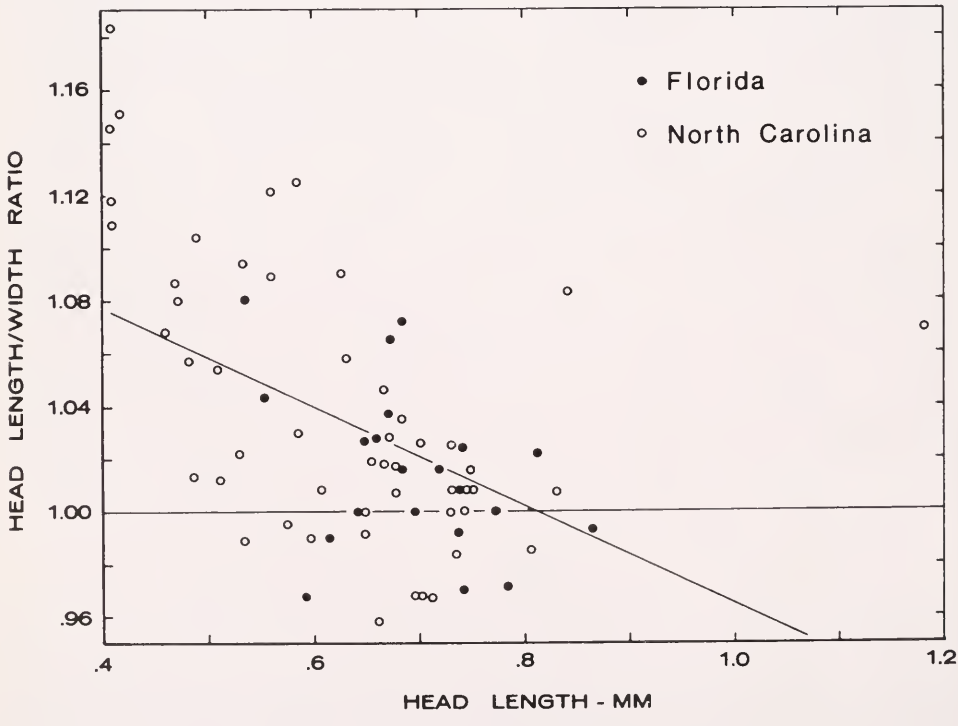
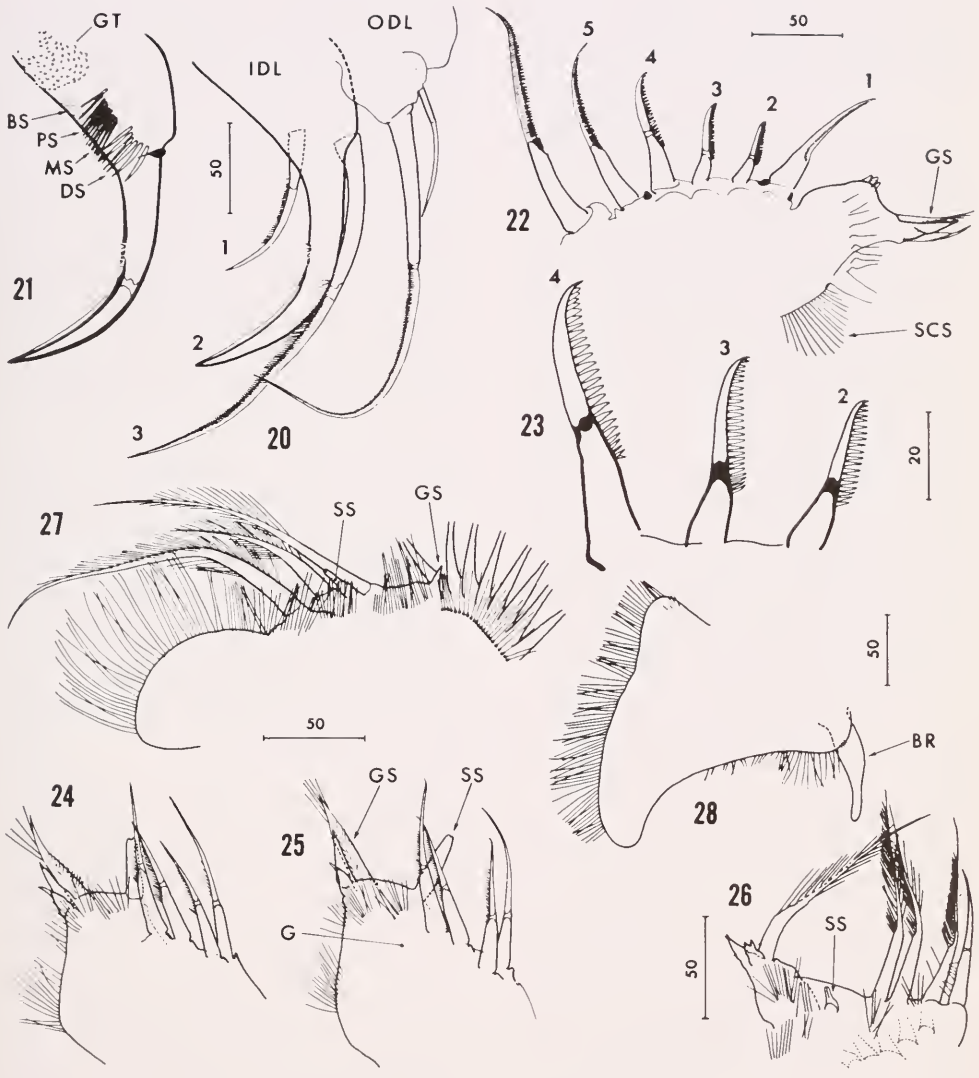


Figure 19. Scattergram and least-squares regression for length/width ratio of the head shield versus the length of the head shield. Florida specimens are from Lake June in Winter, Buck Lake, and Lake Annie. North Carolina specimens are from White Lake and Pages Lake. The regression statistics are given in Table 4.



Figures 20-28. *Eurycercus microdontus* new species from the southern United States. Only those portions of the first five trunk limbs containing potentially diagnostic details have been included. The remaining portions of the trunk limbs seem indistinguishable from those of *E. macracanthus,* fully illustrated in Frey (1973). Figs. 20-23 and 25-27 are drawn from an intact exuvia from Lake Annie, Fla., Samples 2913-2917 — one of the very few recovered in this study. Figs. 24 and 28 are from dissected specimens from White Lake, N. C., Sample 466. 20. Trunk limb I. IDL, inner distal lobe, ODL, outer distal lobe; 1, 2, 3, clasping hooks. 21. Clasping hook 2 of same specimen. GT, grinding tubercles; BS, basal spinules; PS, proximal spinules; MS, marginal spinules; DS, distal spinules. 22. Trunk limb II: gnathobase and adjacent scraping spines. GS, apical gnathobasic setae; SCS, screening setules; 1, 2, 3, 4, scraping spines. 23. Scraping spines 2, 3, and 4 of same specimen. 24. Trunk limb III: gnathobase and adjacent setae. 25. Trunk limb III: gnathobase and adjacent setae. GS, apical gnathobasic setae; SS, sensilla. 26. Trunk limb IV: gnathobase and adjacent setae. SS, sensilla. 27. Trunk limb V: gnathobase and adjacent setae. SS, sensilla; GS, apical gnathobasic setae. 28. Trunk limb VI. BR, respiratory bract.

not yet been worked out for the other three species.

Because the marginal and basal groups of spinules were noticed after the first study (Frey 1973), the four species previously studied were reexamined for these. *E. pompholygodes* and *E. macracanthus* regularly have the marginal spinules, but they have basal spinules mainly in the largest specimens, and even then very few. *E. lamellatus* has marginal spinules irregularly, chiefly in the larger specimens, and basal spinules even less consistently. *E. glacialis* almost never has marginal spinules. Basal spinules are generally absent in small specimens of *E. glacialis* but often abundant in a compact cluster beneath the proximal spinules in large specimens, where they are better developed than in any of the other species. Hence, the inconsistent occurrence and greater variability in number of the marginal and basal spinules suggest that they will be less useful in helping characterize species than the proximal and distal spinules.

Trunk limb II (Figs. 22, 23, 29). Again, the general configuration of this limb is about the same in all species, the chief differences being in scraping spines 2, 3, and 4, and to a lesser extent in the morphology of the gnathobase. In species of the subgenera *Eurycercus* and *Bullatifrons,* spine 2 is the shortest, then spine 3. In *E. microdontus* 4 is distinctly shorter than 1, whereas in *E. lamellatus* and *E. macracanthus* 1 is slightly shorter than 4, and in *E. pompholygodes* 1 and 4 are subequal in length. Hence, any differences in relative length of these scraping spines are species characters rather than subgeneric characters. In *E. glacialis,* by contrast, scraping spines 1, 2, and 3 are all subequal in length, and all are considerably shorter than 4.

The denticles on spines 2, 3, and 4 of *E. microdontus* are long, slender, and not contiguous at their bases, presenting more the appearance of a comb than in any of the other species studied to date (Fig. 23). The number of denticles on all three spines increases steadily with increasing size of animal and all at about the same rate. Differences between the Florida and North Carolina populations are not significant because of a virtual congruence of the 95% confidence limits of the regressions. The most important feature is that in *E. microdontus* the number of denticles on each spine is strongly size dependent, whereas in *E. pompholygodes* the number of denticles on spines 2 and 3 do not change at all with size, and spine 4 even exhibits a slight but significant decrease in denticle number with increasing size of animal (Fig. 29). Regretfully, regressions have not yet been established for *E. lamellatus* and *E. macracanthus,* and hence it is not known if these differences in regression of tooth number versus size are characteristic of species or subgenera.

The slight differences in length and structure of the three setae at the apex of the gnathobase are vague and not yet resolved on any useable basis. Their details are frequently obscured by the setae of the gnathobasic filtering plate. In the crescent of blunt pyramidal denticles on the edge of the gnathobase toward the scraping spines, the denticle that is considerably larger than the others in *E. macracanthus* and *E. pompholygodes* is scarcely larger than the others in *E. microdontus.*

Trunk limb III (Figs. 24, 25). Of the articulated setae adjacent to the gnathobase, 2 and 3, counting from the gnathobase, are considerably shorter than 1 and 4 in both the Florida and North Carolina populations. In *E. pompholygodes* and *E. macracanthus* also the middle setae are shorter than the lateral ones, but not nearly to the extent as in *E. microdontus.* In *E. lamellatus* and *E. glacialis* setae 1 and 2 are longer than 3 and 4. Otherwise trunk limb III is relatively undifferentiated at the species level. The setation on the gnathobase seems less well developed in *E. microdontus* than in the other species, which may be related to its smaller size.

Trunk limb IV (Fig. 26). There are no obvious differences in *E. microdontus* from the other species studied. The sensilla is possibly a little smaller relatively, and the two shorter setae at the tip of the gnathobase seem a little different in structure. However, the latter differences are difficult to resolve in any meaningful manner.

Trunk limb V (Fig. 27). The middle seta of the three near the sensilla is markedly shorter than the lateral ones, as in *E. macracanthus* and *E. pompholygodes*. Since the latter species are in a different subgenus than *E. microdontus*, the relative length of these setae represents specific rather than subgeneric differentiation. In the specimen drawn, only one gnathobasic seta was visible. Among the largest specimens dissected, generally two gnathobasic setae could be made out, sometimes only one, never three. Because of the difficulty in resolving such small details on dissected limbs, it is not certain that any of the limbs had only one seta. Fresh exuviae are necessary to decide this.

Both the Florida and North Carolina populations always had 8 "soft" setae and 9 gnathobasic setae on trunk limbs III and IV, and 7 and 8, respectively, on trunk limb V (Table 5). This is the general pattern in all known species of the subgenera *Eurycercus* and *Bullatifrons*, but all species except *E. microdontus* – particularly *E. pompholygodes*, for which available data are most extensive – exhibit some variability in these numbers from specimen to specimen and even between right and left limbs of the same specimen.

Trunk limb VI (Figs. 4, 28). This limb seems unusually large in *E. microdontus*, compared with the other species. It consists of an expanded triangular plate attenuated and narrowly rounded ventrally, and a respiratory bract attached posteriorly at the base. The anterior edge of the plate is provided with a double row of long setae (only one row is shown in Fig. 28) along its entire length except at the ventral tip. The proximal half of the posterior margin is provided with a single row of more widely spaced setae, which increase in length proximally toward the respiratory bract. The shape shown in Figure 4 of the whole specimen is more representative than that of the isolated limb in Figure 28, which was somewhat distorted by dissection and mounting. Both the

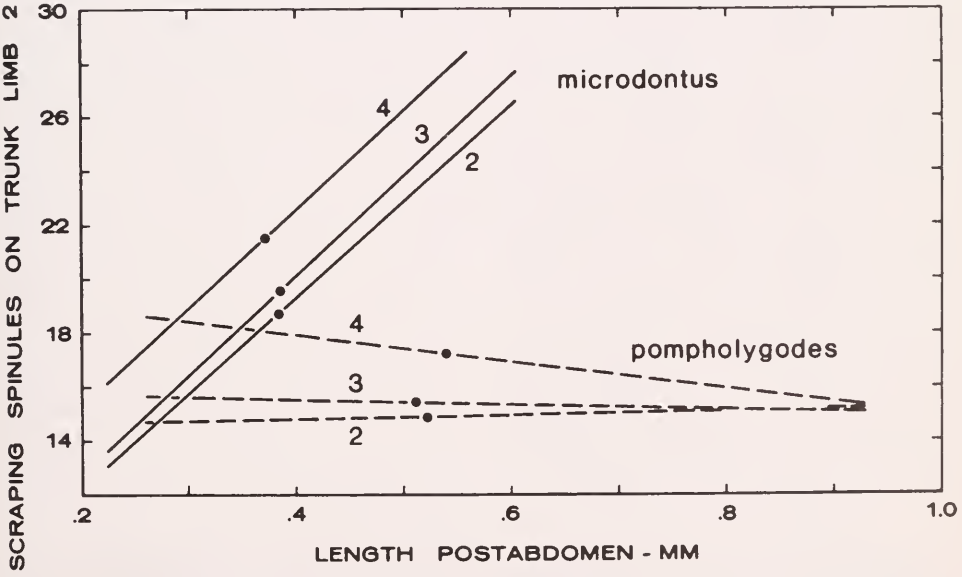
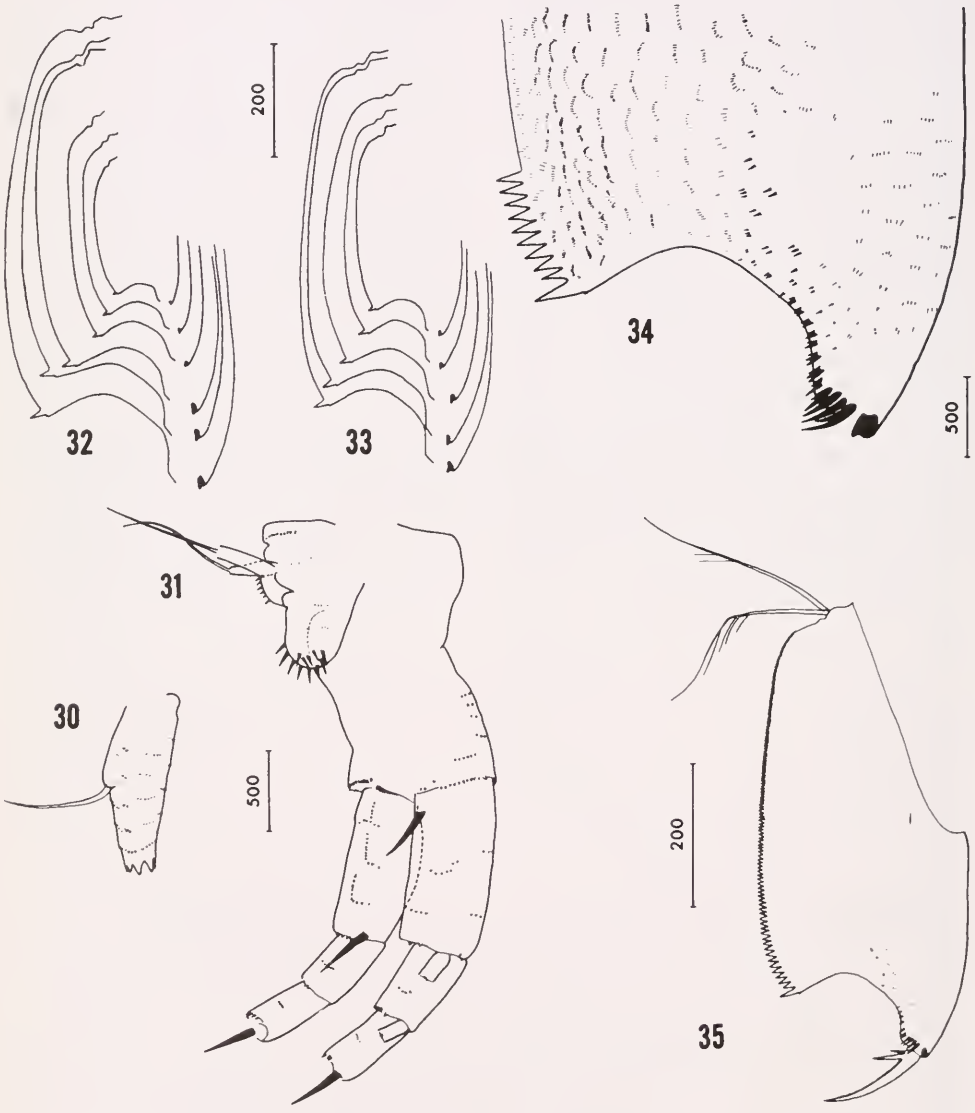


Figure 29. Least squares regressions of the number of denticles on scraping spines 2, 3, and 4 of trunk limb I versus length of postabdomen for the combined populations from White Lake and Lake June in Winter. For each regression line, the dot represents the mean of the two variables, and the length of the line corresponds to the range in length of the postabdomens. *E. pompholygodes* is a species in the subgenus *Bullatifrons* from northern Sweden (Frey 1974). These are the only two species for which these regressions have been worked out. See Table 4 for the regression statistics for *E. microdontus* for the individual localities.

Florida and North Carolina populations have the same shape and general morphology. Some of the smaller White Lake specimens, such as the one drawn (Fig. 4), were striking in the clarity with which trunk limb VI was visible, hanging vertically like a curtain on either side of the midline between trunk limbs V.



Figures 30-35. *Eurycercus microdontus* new species from the southern United States. 30. Antennule from Lake Annie, Fla., Samples 2913-2917. 31. Antenna from Lake Annie, Fla., Samples 2913-2917. The swimming setae are not shown. 32. Outline drawings of isolated postabdomens from North Carolina. Only the distalmost tooth is shown. The three largest specimens are from Pages Lake, the three smallest from White Lake. 33. Outline drawings of isolated postabdomens from Florida. The middle specimen is from Lake Annie, the other four from Lake June in Winter. 34. Distal end of postabdomen, Lake June in Winter, Fla. Note the shallow anal embayment, the truncation of the toothed zone, and the stout spines distally as well as along the mid-lateral surface. 35. Postabdomen and claw from exuvia from Lake Annie, Fla.

Table 5. Frequency of "soft" and gnathobasic setae on trunk limbs III, IV, and V of *E. microdontus*. The numbers are based mainly on dissected specimens and include both the right and left limbs of the same specimen where possible.

		Number of setae					
		Florida			N. Carolina		
Limb No.	Kind of setae	7	8	9	7	8	9
III	Soft		15			17	
	Gnathobasic			19			17
IV	Soft		20			19	
	Gnathobasic			20			14
V	Soft	16			18		
	Gnathobasic		19			17	

Postabdomen (Figs. 2, 4, 32-38). The most distinctive characters of *E. microdontus* are the large number of very minute teeth along the dorsal edge of the postabdomen and the very steep rate of increase in number of these teeth as the specimens become larger. Whereas in other morphological characters there are no significant differences between the Florida and North Carolina populations, the regressions for length of the postabdomen (Fig. 36) and number of postabdominal teeth (Fig. 37) as functions of size are statistically different. The meaning of these differences between the two populations cannot be interpreted at present. If subsequent studies suggest the desirability of separate taxonomic recognition of the two populations, then the characters of the Florida population will have to be regarded as those of the species *Eurycercus microdontus* sensu strictu.

The rate of increase in tooth number with size of animal is much greater than in any other species of *Eurycercus* studied to date, resulting in numbers greater than 140 in the largest specimens from Florida. This is the first species known in which the relationship between tooth number and size obviously is not linear but sigmoid. No attempt was made to fit higher order equations to the data, but rather lines were drawn freehand to show the general relationship (Fig. 37).

During the pre-reproductive instars tooth number increases very slowly if at all. During the early reproductive instars tooth number increases precipitously — as many as 34 teeth in a single instar — and in the later reproductive instars the rate of increase levels off once again. For those specimens in which the number of teeth in the next instar could be counted, the increase (or decrease in a few instances) in tooth number has been plotted against the length of the postabdomen in the current instar (Fig. 38). Also given are the linear regression lines of tooth number versus length of postabdomen for the populations from Lake June in Winter, White Lake, and Pages Lake. The data establish the mechanism for the production of a sigmoid relationship, namely a much greater increase in tooth number per instar during the intermediate instars. Figure 38 also demonstrates that there is no significant difference in rate of increase between the neighboring populations from White Lake and Pages Lake.

The shape of the postabdominal teeth likewise is different between the two populations. In North Carolina specimens the teeth are more triangular and saw-tooth in appearance, whereas in Florida specimens they are elongate, relatively straight-sided, and closely packed together.

The shape of the postabdomen is more variable for this species than for any of the other four species studied to date (Frey 1973, 1974). Sometimes the dorsal margin is flattened as in *E. glacialis*, at other times with a major curvature distally as in *E. macracanthus*. The anal groove is broader and shallower than in any of the other four species. The toothed zone is abruptly truncate distally, as is characteristic of the subgenera *Eurycercus* and *Bullatifrons*.

Postabdominal claw (Fig. 35). The gross morphology of the claw is quite similar in all species of *Eurycercus*. As in the other four species studied previously (Frey 1973, 1974), the number of denticles on the postabdominal claw of *E. microdontus* increases with length of the postabdominal claw and hence with size of animal. The number of

denticles is less for a given claw length than in the other four species over the size range represented, but the rate of increase is as great as in *E. glacialis* and considerably greater than in the other three species. Seemingly slight differences in relative proportions of the claw, curvature, and length and stoutness of the two basal spines cannot be quantified at present.

Intestine (Fig. 4). As in all other known species of the subgenera *Eurycercus* and *Bullatifrons*, the intestine has a single loop and a well-defined caecum near the base of the postabdomen.

BIOLOGY

a) *Growth, maturity, and instar analysis*

The samples from White Lake and Lake June in Winter are not large enough for the kind of instar analysis accomplished in previous studies (Frey 1973, 1974) Even when the data are combined into size classes of 2 scale-units, the size-frequency distributions are discontinuous, and the sub-divisions may not correspond precisely to the individual pre-reproductive instars (Fig. 39).

Instar I is reasonably distinct, as in all populations of *Eurycercus* studied to date. Fifteen specimens had a size range of .58-.68 mm, with a mean of roughly .63 mm. What seems to be instar II (Fig. 39) has a size range of .75-.90 mm, with a mean of .83 mm for 41 specimens. This gives a growth ratio (.83/.63) of 1.29, which is larger than for any other species of *Eurycercus* studied to date except *E. glacialis* (Frey 1973). The two populations analyzed separately give growth ratios of 1.31 for Lake June in Winter (mean length .82 mm in Instar II for 21 specimens) and 1.27 for White Lake (mean length .79 mm for 20 specimens). The other isolated parts of the length-frequency distribution, assuming that they represent individual instars, yield similar high growth ratios compared with the other species.

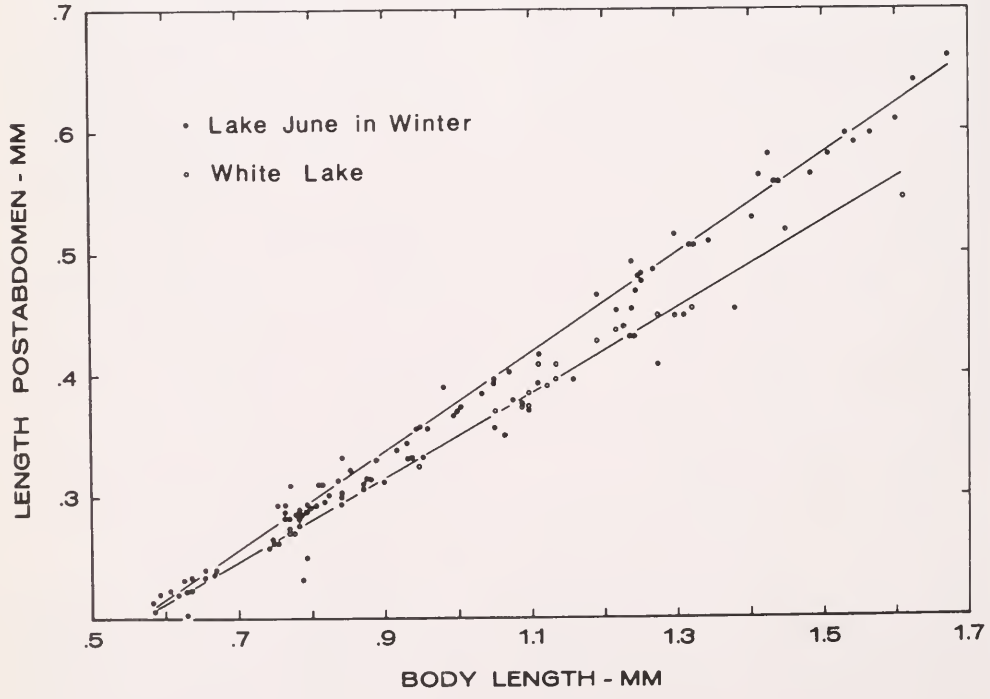


Figure 36. Scattergrams and least-squares regressions between length of postabdomen and length of animal for *E. microdontus*. Regression statistics are given in Table 4. The regressions for Lake June in Winter and White Lake are significantly different.

Either *E. microdontus* actually has fewer pre-productive instars (seemingly only three in White Lake and four in Lake June in Winter) than the other species, including the equally small species *E. macracanthus,* or else the data are misleading because of the vagaries of small sample size. However, these small numbers of pre-reproductive instars are not unreasonable, because Bottrell (1975) has found that for Cladocera in general, the number of pre-reproductive instars increases with size of species. My interpretation of the various species of *Eurycercus* parallels his findings quite closely (see below).

Previous studies have shown that 1 1/2 to 2 instars are required for the ovaries to develop to reproductive capacity (Frey 1973, 1974). The specimens from White Lake were so heavily pigmented from the filamentous algae in the collection that the stage of development of the ovaries could not be determined. For Lake June in Winter, specimens in the first two instars, as interpreted in Figure 39, either had the ovaries not visible at all, or the oocytes were extremely small. In instar III only a couple of the largest specimens had oocytes visible at the magnification used, whereas in instar IV most specimens in the latter half of their molt cycle had enlarged oocytes surrounded by yolk material, indicating that they would have become reproductive after the next molt, which is in fact what was happening on a population basis. The number of pre-productive instars in other species of *Eurycercus* increases from 5 in *E. macracanthus* and *E. pompholygodes* to 6 in *E. lamellatus* to possibly 7 in *E. glacialis,* cor-

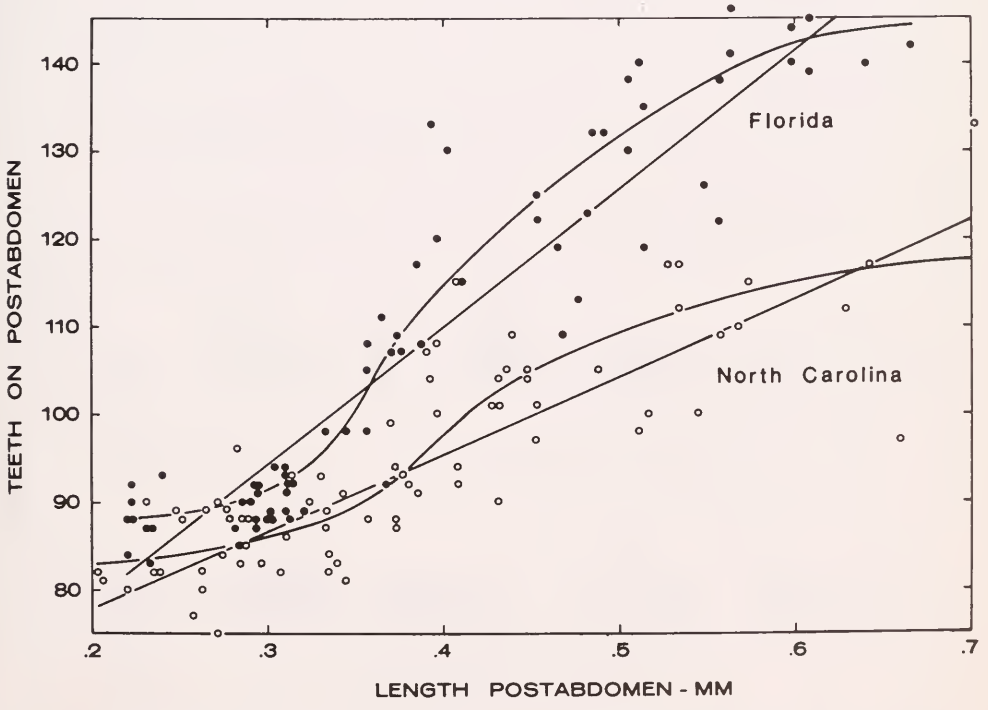


Figure 37. Scattergrams and least-squares regressions between number of postabdominal teeth and length of the postabdomen for *E. microdontus* from Florida (Lake June in Winter) and North Carolina (White Lake and Pages Lake). The relationship obviously is not linear, as shown by the poor fit of the regression lines to the data. The sigmoid curves have been drawn in freehand to suggest a more likely relationship. Even on a linear basis, the populations from Florida and North Carolina are significantly different.

responding to an increase in size at which reproduction begins. It seems rather unlikely from this size relationship that the Lake June in Winter population would have only 4 pre-reproductive instars. Nevertheless, it is definite from the data at hand that the White Lake specimens begin reproduction at a size corresponding to the last pre-reproductive instar in the population from Lake June in Winter, and hence there is a distinct possibility that they have one fewer pre-reproductive instar. Certainly, the White Lake specimens become reproductive at a smaller size than any other known population of *Eurycercus*. As is typical of the small species of *Eurycercus*, all specimens larger than the size at which parthenogenetic reproduction begins are reproductive. There is essentially no overlap in size distribution of the last pre-reproductive instar and the first reproductive instar, as there is in *E. lamellatus* and *E. glacialis* (Frey 1973).

b) *Egg size and fecundity*

The average lengths (mean ± standard deviation) of the major and minor axes of 7 recently released parthenogenetic eggs from a total of 3 individuals in the Lake June in Winter sample are 218 ± 11.7 μm and 183 ± 8.9 μm, respectively, with an axis ratio of 1.19 and an approximate mean volume of $3.8 \times 10^6 \mu m^3$. Hence. the egg volume is almost identical to that of *E. macracanthus* — the next smallest species of *Eurycercus* — although the axis ratio is considerably smaller, meaning that the eggs are relatively less elongate.

For 16 parthenogenetic females 1.19-1.67 mm long with closed brood pouches, the regression of egg number against body length

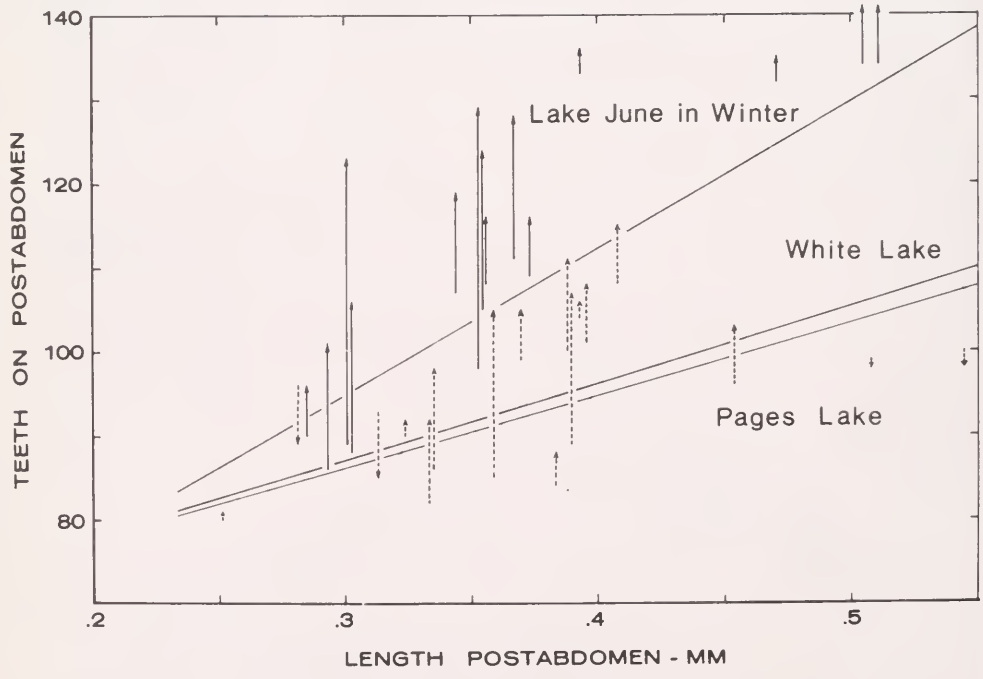


Figure 38. Increase (or decrease) in postabdominal tooth number of single specimens from the present instar to the next instar, plotted against length of postabdomen in the present instar. In both the Florida and North Carolina populations the biggest increase in tooth number tends to occur in the early reproductive instars. Also included for orientation are the least-squares regressions for the two populations from North Carolina (which do not differ from each other) and for the one from Florida (which is significantly different from the other two).

has a slope of .1899, a y-intercept of −21.51, and a correlation coefficient of .90. Included are 7 specimens from White Lake, 6 from Lake June in Winter, 2 from Lake Jackson, and 1 from Buck Lake. The specimens from White Lake all measured 1.31 mm or smaller, those from the other localities 1.34 mm or larger. Nevertheless, the scattergram indicates only a single relationship between fecundity and body length. What this suggests is that primiparous specimens from Lake June in Winter by virtue of being larger in size than the White Lake specimens at the onset of reproduction have larger broods consonant with their size. An anomalous record not included in the regression is a female 2.23 mm long from Southern Pines, N. C., which contained only 11 embryos, whereas according to the regression equation there should have been about 20.

This is a steep rate of increase in reproductive potential, which is almost identical in slope and displacement to that of the *E. macracanthus* population from Siberia. The latter, in the subgenus *Bullatifrons,* has a broadly rounded shell, which is only moderately arched dorsally over the brood pouch (cf. Fig. 1 in Frey 1973 and Figs. 1, 3, and 4 in Frey 1974). In *E. microdontus,* on the other hand, the brood pouch is compressed laterally by the development of the sharp dorsal keel (Fig. 3), but this is compensated for by the high arching of the shell over the brood pouch, resulting in the brood pouch capacity of the two species being almost the same in spite of their vastly different morphology.

As is true of all other parthenogenetic populations of *Eurycercus* studied to date except *E. glacialis* (Frey 1973, 1974), the great majority of individuals in a collection

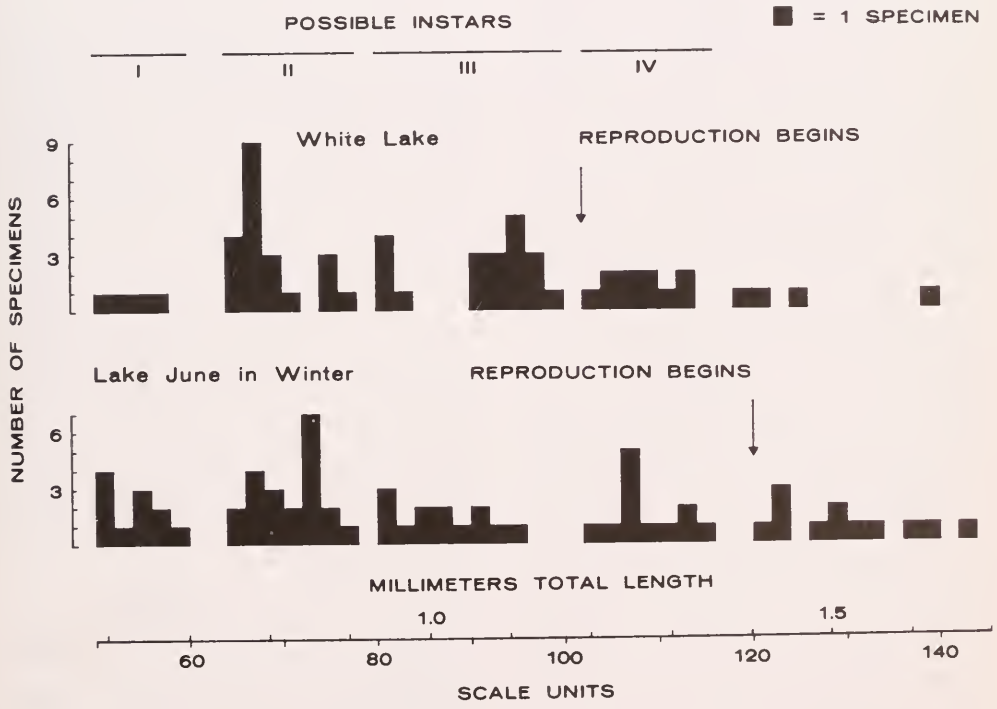


Figure 39. Length-frequency distributions of the major samples of *E. microdontus* from White Lake, N. C., and Lake June in Winter, Fla. The data have been combined into classes of 2 scale units because of the small number of specimens.

are pre-reproductive. Of the 208 intact specimens of *E. microdontus* from 12 localities (Table 3), only 28 had eggs or embryos in their brood pouches, 17 with closed brood pouches. Reproduction in this species, or at least in the White Lake population, begins at a smaller size than in any other known species of *Eurycercus*. The smallest reproductive specimen measured 1.19 mm, and 5 other specimens were less than 1.3 mm long, which is the smallest size previously known at the onset of reproduction, in the Siberian species *E. macracanthus* (Frey 1973). Other sizes at onset of reproduction are 1.34 mm in Buck Lake, 1.39 mm in Lake Jackson, and 1.41 mm in Lake June in Winter.

c) *Gamogenesis*

Males and ephippial females of this species are unknown. All individuals collected in Florida in December 1972 were parthenogenetic, even though virtually all species of chydorids in northern Indiana had been gamogenetic for some weeks. Shan's study (1974) on *Pleuroxus denticulatus* demonstrated that southern populations initiate gamogenesis at long photoperiod rather than short, and this seems true for the *Bullatifrons* species (and probably also *E. microdontus)* in the southern states. Chien (1969) illustrated a male (mislabelled female) of *Bullatifrons* from Mississippi collected on 10 May 1967. One of two specimens collected by Bunting in the Santeetlah Reservoir, N. C., on 25 May 1969 (Table 1) was gamogenetic. A population from near Clarendon, Ark., was gamogenetic on 30 March 1959. In early May 1974 populations in a pond near Reelfoot Lake, Tenn., and in Courtebleau Bayou, La., were gamogenetic, although populations at Chien's localities in Mississippi were parthenogenetic. These are all the known records for gamogenesis of *Eurycercus* in the southern states. They strongly suggest that gamogenetic individuals of *Eurycercus* (and probably other Cladocera as well) in the lower North Temperate latitudes should be looked for in the spring during increasing photoperiod rather than in the autumn.

d) *Distribution and abundance*

Although the genus *Eurycercus* is widespread in the southern United States, the species *E. microdontus* is presently known only from localities within 300 km of the Atlantic and Gulf coasts, all the more inland records being of *Bullatifrons* sp. (Fig. 1). *E. microdontus* occurs in quite large lakes (Lake June in Winter, Lake Jackson, and White Lake) as well as in smaller water bodies of the farm-pond variety (the two localities of D. L. Dycus in Georgia). Because there have been very few studies of Cladocera in this part of North America, the records are only suggestive of the actual distribution and abundance. I suspect that the smaller water bodies, such as ponds, backwaters, slow streams, etc., particularly those with an abundance of macrophytes, and hence some protection against predation by fishes, will yield many records of the species when they are studied intensively.

ACKNOWLEDGMENTS

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COPEPODA OF NORTHERN MISSISSIPPI WITH A DESCRIPTION OF A NEW SUBSPECIES

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ABSTRACT

Variable types of Mississippi surface waters north of 33° north latitude were examined qualitatively for the occurrence of calanoid and cyclopid copepods. A total of 283 collections was made from 59 sites from August 1972 through July 1973. Samples were taken once each season. Twenty-five species in four families, including three which were represented by two subspecies, were taken in the study area. A new subspecies of *Diaptomus bogalusensis* is described. *Diaptomus pallidus* and *Tropocyclops prasinus* and its subspecies *T. p. mexicanus* were the most numerous and widespread calanoid and cyclopoid copepods taken. Seventeen species are new records for Mississippi.

Despite their importance, the free-living, freshwater copepods have been given relatively little attention in the United States. In Mississippi, in particular, there is a lack of systematic work on this group. Marsh (1907, 1912, 1929) noted the presence in Mississippi of *Macrocyclops albidus, Eurytemora affinis, Diaptomus mississippiensis* and *D. pallidus.* Eddy & Simer (1928) also recorded *Cyclops bicuspidatus* and *Mesocyclops leuckarti* from Mississippi. Wilson & Yeatman (1959) specifically mention the presence in Mississippi of *D. virginiensis,* and Grantham (1958) noted the presence of *Mesocyclops edax* and *D. mississippiensis.* One other rare calanoid, *Epischura fluviatilis,* was recently taken from Pickwick Reservoir on the Mississippi-Alabama border by D. L. Bunting (personal communication).

The current investigation surveys and updates the knowledge of the cyclopoid and calanoid copepods in surface waters of Mississippi north of 33° north latitude.

MATERIALS AND METHODS

Samples were taken with a 30.5 cm plankton net using number 25 silk bolting cloth. Collections were made at 59 sites once per season for a total of 283 collections (some sites collected in several locations). Samples were taken from 13 lakes, nine ponds, nine streams, 10 rivers, 10 ditches and other intermittent waters, and nine swamps, sloughs or small oxbow lakes. Six Mississippi river drainages were sampled: Tombigbee, Big Black, Pearl, Tennessee, Yazoo and Upper Mississippi including the Horn, Hatchie, and Wolf systems. The study area covered approximately 53,000 km^2 and 40 counties. Samples were taken from the surface to a depth of approximately 2.0 m or less depending upon the depth of the water, except that in the five large reservoirs, samples were taken to depths of approximately 5.0 m. Specimens were killed in 5% formalin and preserved in 70% ethanol. Dissected and whole specimens were mounted in glycerin jelly. Species identification and terminology follows that of Wilson and Yeatman (1959).

At each site dissolved oxygen content, temperature and pH measurements were taken using a YSI oxygen meter, model 51A and Coleman Metrion IV pH meter.

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RESULTS

Twenty-five species, three of which were represented by two subspecies, were taken in the study area. One undescribed species and a new subspecies, *Diaptomus bogalusensis marii,* were included in the collections. The order Calanoida was represented by three families: Centropagidae (one genus with one species), Temoridae (one genus with one species) and Diaptomidae (one genus with nine species) The order Cyclopoida was represented by only one family, the Cyclopidae, with six genera and 14 species.

Seven species, including *Diaptomus sanguineus, D. virginiensis, Osphranticum labronectum, Eurytemora affinis, Cyclops bicuspidatus thomasi, C. crassicaudis brachycercus* and *Macrocyclops ater* were taken only during the winter and/or early spring sampling period when temperatures were considerably lower and water levels were higher. Four species, *Diaptomus dorsalis, Macrocyclops fuscus, Mesocyclops tenuis* and *Eucyclops agilis montanus* were found only in the summer collections. All other species were present throughout the year with the exception of two species which appeared in three of four collections.

Oxygen levels ranged from a low concentration of 0.4 ppm to a high of more than 15.0 ppm without any evident effect on the number or diversity of copepod species. The same was true of the pH values for the various bodies of water which ranged from a low of pH 5.4 to a high of pH 9.7. Temperatures ranged from 19.5°C to 34.0°C in the summer, 0.0°C to 9.0°C in winter and 8.5°C to 23.5°C in the early spring.

LIST OF SPECIES

Order Calanoida
- Family Centropagidae
  1. *Osphranticum labronectum* Forbes, 1882
- Family Temoridae
  2. *Eurytemora affinis* (Poppe), 1880
- Family Diaptomidae
  3. *Diaptomus dorsalis* Marsh, 1907
  4. *D. siciloides* Lilljeborg, 1889
  5. *D. sanguineus* Forbes, 1876
  6. *D. virginiensis* Marsh, 1915
  7. *D. pallidus* Herrick, 1897
  8. *D. mississippiensis* Marsh, 1894
  9. *D. reighardi* Marsh, 1895
  10. *D. bogalusensis marii* new subspecies
  11. *D.* sp.

Order Cyclopoida
- Family Cyclopidae
  12. *Paracyclops fimbriatus* (Fischer), 1853
  13. *P. fimbriatus poppei* (Rehberg), 1880
  14. *Eucyclops prionophorus* Kiefer, 1931
  15. *E. speratus* (Lilljeborg), 1901
  16. *E. agilis* (Koch), 1838
  17. *E. agilis montanus* (Brady)
  18. *Tropocyclops prasinus* (Fischer), 1860
  19. *T. prasinus mexicanus* Kiefer, 1938
  20. *Cyclops vernalis* Fischer, 1853
  21. *C. bicuspidatus thomasi* Forbes, 1882
  22. *C. crassicaudis brachycercus* Kiefer, 1929
  23. *C. varicans rubellus* Lilljeborg, 1901
  24. *Mesocyclops edax* (Forbes), 1891
  25. *M. tenuis* (Marsh), 1909
  26. *Macrocyclops fuscus* (Jurine), 1820
  27. *M. albidus* (Jurine), 1820
  28. *M. ater* (Herrick), 1882

ECOLOGICAL AND DISTRIBUTIONAL NOTES

Genus *Osphranticum* Forbes

Osphranticum labronectum was collected during the winter and early spring periods when water temperatures ranged from 2.5°C to 14.5°C. It occurred in shallow sloughs with little or no current, connected to or immediately adjacent to rivers and creeks. The species was taken from the Yazoo, Big Black and Pearl river drainages.

Genus *Eurytemora* Giesbrecht

Eurytemora affinis was collected during early spring in waters that ranged from

14.0°C to 16.5°C It was found in flooded oxbow lakes adjacent to and continuous with the Mississippi River.

Genus *Diaptomus* Westwood

Diaptomus dorsalis was found once in considerable numbers in the late summer collection. It was taken from a large creek with little or no current, in the Yazoo drainage.

D. siciloides was collected during all seasons, except late summer, in large lakes, streams and rivers of the Yazoo and Mississippi drainages.

D. sanguineus was found during the winter and early spring periods in the Yazoo and Pearl River drainages. It occurred in slow moving streams and sloughs and in a flooded field adjacent to a farm pond, but was not taken from the pond itself.

D. virginiensis was found in sloughs adjacent to rivers of the Yazoo drainage during the winter collection period. Water temperatures at the collection sites ranged from 3.5°C to 7.5°C.

D. pallidus occurred in all habitats sampled, and within a wide range of pH, temperature and dissolved oxygen values.

D. mississippiensis was collected during all seasons in the Yazoo, Tombigbee, Tennessee and Big Black river drainages. It was predominantly lentic, appearing most often in lakes and ponds, but was not taken from creeks.

D. reighardi was abundant and widespread and was found during all seasons in all drainages and in all types of habitats. Two-thirds of the collections of this species were made from lakes and ponds.

Description of New Subspecies

D. bogalusensis marii new subspecies

(Figs. 1-6)

Occurrence: This species was taken from all drainages and during all seasons in northern Mississippi. It was found most often in lakes, ponds and other standing waters, but was collected on rare occasions from lotic habitats.

Type lot: Holotype female, USNM 151227, paratypes, male and female, USNM 151228 and 151229, from Tishomingo St. Pk. Lake, Tishomingo Co., Miss.

Diagnosis: Female. Average length of 15 preserved specimens 1.11 mm (0.93 mm-1.30 mm). Metasome (Fig. 1) with head rounded; greatest width at posterior portion of first metasomal segment and second metasomal segment; width about 37% of total length of metasome. Metasome tapering gradually, especially distal to metasomal segment 3. Metasomal segments 5 and 6 not separated dorsally, "wings" of segment 6 directed posteriorly with small sensillum on lateral posterior corners.

Urosome (Fig. 2) 3-segmented, approximately 35% of length of metasome. Genital segment asymmetrical to nearly symmetrical, left side rounded, symmetric, right side more flattened on posterior margin with sensillum located on anterior margin. Segment 2 shorter than segment 3, caudal rami equal to or slightly longer than segment 3. Inner margins of caudal rami bearing hairs.

Antennules reaching beyond distal ends of caudal rami setae, one seta on segments 11 and 13-19.

Maxillipeds (Fig. 3) with distal lobe of basal segment bearing three setae.

Leg 5 (Fig. 6) basipod 1 subglobular and about as long as wide. Basipod 2 subtriangular and slightly longer than wide with lateral seta on external margin reaching along outside margin. Basipods 1 and 2 – 1.05; exopod 1 – 1.00; and exopod 2 – 1.08 (proportional lengths). Exopod 2 base slightly more than one-third of length. Exopod 2 bearing no latteral seta. Exopod 3 represented by two lateral setae on proximal lateral margin of exopod 2. Length of setae variable, but outer usually at least twice length of inner. Endopod reaching beyond base of exopod 2 with distal end bearing numerous fine setae and two longer setae, outer longer and its length slightly greater than greatest width of endopod. Endopod ends in pointed protuberance.

Male. Average length of six preserved specimens 1.03 mm (0.9 mm – 1.11 mm).

Metasome similar to female.

Urosome symmetrical.

Left antennule as in female. Right anten-

nule (Fig. 4) with spines of segments 8 and 12 shorter than width of their respective segments; spine 12 shorter than 8. Spine of segment 10 nearly as long as width of segment and spine of segment 11 longer than width of segment 11. Spine on segment 13 almost reaching proximal margin of segment 15. Spinous process present on segments 15 and 16 with 15 the larger.

Leg 5 (Fig. 5) with right posterior face of basipod 2 bearing blunt, bifid spine on distal margin. Exopod 1, inner distal margin with small rounded lamella. Exopod 2 inflated anteriorly, spine about as long as width of segment at spine. Claw about as long as exopod, sickle-shaped, very robust.

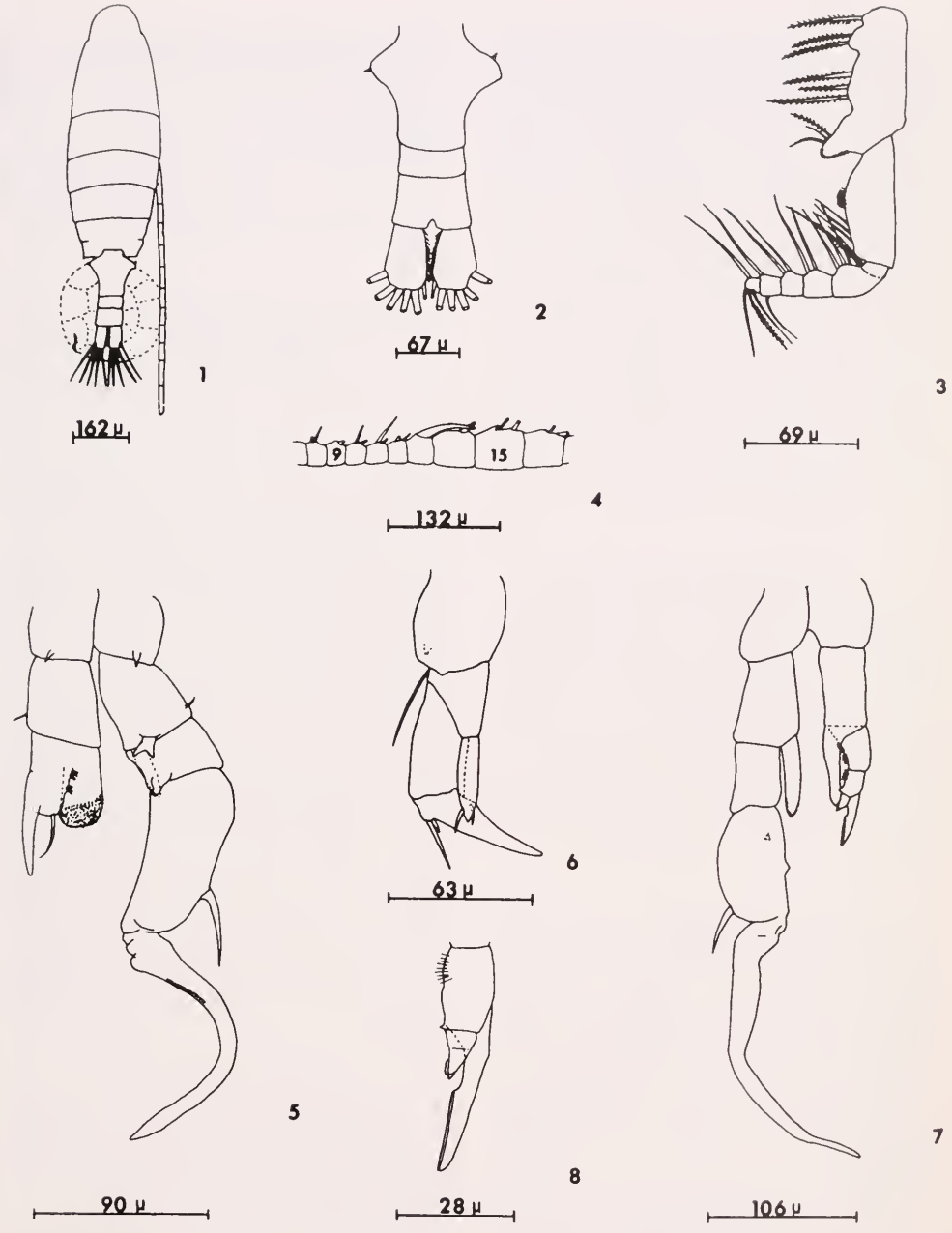
Leg 5 left (Fig. 5) (excluding process) reaching to end of right exopod 1. Basipod longer and wider than exopod. Exopod segments 1 and 2 incompletely separated. Exopod 1 rounded inner pad and proximal pad of the second exopod segment with long hair. Exopod 2 with two prominent processes; the outer process stouter and longer than exopod. Inner, slender process about 80% of length of outer. Endopod very large and slightly longer and as wide as exopod. Distal end of endopod covered with many short, stout hairs.

Systematic position: This subspecies appears to be an intermediate form between *D. sinuatus* Kincaid, 1953 and *D. bogalusensis* Wilson & Moore, 1953, but more closely related to the latter. In the female this relationship is indicated by the nature of the genital segment of the urosome. The right side of this segment in *D. sinuatus* forms a small conical protuberance while in *D. bogalusensis* the right side is formed into a large laterally directed protuberance. This protuberance in *D. b. marii* is larger than in *D. sinuatus* but much more symmetrical and shorter than in *D. bogalusensis*. The fifth leg of *D. b. marii* differs from the other two species in that the spines representing the vestigal third exopod segment are unequal in length, the outer being much longer.

In the male the major areas of difference lie in the nature of the right antennule and the fifth legs. In *D. sinuatus* the spine on segment 13 of the right antennule reaches the proximal margin of segment 15. In *D. b. marii* this spine almost reaches the proximal margin of segment 15 but in *D. bogalusensis* it reaches just beyond the middle of segment 14. The fifth leg of *D. b. marii* presents a number of similarities to *D. sinuatus* and *D. bogalusensis*. *D. b. marii* and *D. sinuatus* have a triangular lamella on the distal inner margin of right exopod 1. *D. b. marii* and *D. sinuatus* both have a small bifid spine on the distal margin of right basipod 2. The claw of *D. b. marii* is unlike that of the other two species in being sickle-shaped and robust. The left exopod 2 is quite similar in all three groups, with *D. b. marii* and *D. bogalusensis*, having a somewhat longer short spine than is present in *D. sinuatus*. Exopods 1 and 2 of the left leg are not completely separated in *D. b. marii* and *D. bogalusensis* while they are completely separated in *D. sinuatus*. The left endopod is similar in *D. b. marii* and *D. bogalusensis* but that in *D. sinuatus* is much longer and narrower. These three groups presently are found only in the southeastern United States: *D. bogalusensis* in Louisiana, *D. b. marii* in northern Mississippi and *D. sinuatus* in northwestern Florida. The morphological and geographical nature of *D. b. marii* indicates there may be a very close relationship between these three groups. With further collecting and a better understanding of their ranges, this relationship should be clarified.

Descriptive Notes on *Diaptomus* sp. (Figs. 7, 8)

Male right first antennae without spinous process on segment 14 or 15. Exopod 2 of right fifth leg (Fig. 7) with outer margin rounded and inner margin with small stout spine. Claw of exopod 2 angled in two places and much longer than exopod. Endopod of right leg 5 enlarged as in *D. mississippiensis*. Left leg 5 terminal segment (Fig. 8) with two processes, outer more anterior process nearly as long as entire exopod with distal two-thirds of inner margin flattened. Inner and more posterior process triangular and less than one-half length of outer. Endopod reaching almost to distal end of short inner process. Average length of male 0.80 mm.



Figs. 1-8. *Diaptomus bogalusensis marii* new subspecies. 1. Female dorsal view. 2. Female urosome. 3. Female maxilliped. 4. Male right first antennae segments 8-16. 5. Male fifth leg posterior view. 6. Female fifth leg. *Diaptomus sp.* 7. Male fifth leg anterior view. 8. Male fifth leg detail of processes of left exopod two.

Occurrence: This copepod was found during all seasons and in all drainages except the Tombigbee. It was collected from all types of habitats with the exception of swamps and sloughs. More than 70% of the collections of this species were taken from lakes and ponds.

Remarks: According to H. C. Yeatman (personal communication), this species was being described by the late M. S. Wilson of Anchorage, Alaska. It has been collected by several other workers, from southeastern United States, including Dr. Yeatman and Dr. D. L. Bunting of the University of Tennessee at Knoxville. At this time and until Wilson's unpublished papers are studied, its status is uncertain.

Genus *Paracyclops* Claus

Paracyclops fimbriatus was found during all seasons in all types of habitats. It was present in all drainages except that of the Big Black and Pearl Rivers.

P. fimbriatus poppei was much less common than *P. fimbriatus,* appearing only during the winter and early spring collections in creeks, rivers, and intermittent waters of the Yazoo River drainage.

Genus *Eucyclops* Claus

Eucyclops prionophorus was collected only four times. It was found in late summer and early spring in the Yazoo and Tennessee River drainages. *E. prionophorus* was taken from one lake, two creeks and one pond.

E. speratus was found throughout the year in all types of habitats except rivers. It was present in the Yazoo and Tombigbee drainages.

E. agilis was present in all types of habitats and in all drainages throughout the year. It was one of the most common and widespread cyclopoid copepods encountered in northern Mississippi.

E. agilis montanus is much smaller and characterized by shorter caudal rami which are not more than 2.5 times their width. It was taken from swamps, sloughs and intermittent waters of the Yazoo River drainage.

Genus *Tropocyclops* Kiefer

Tropocyclops prasinus was widespread in all habitats and drainage systems. It was taken during the late summer, winter, and early spring periods.

T. prasinus mexicanus was found in all drainage systems, all types of habitats, and during all seasons.

Genus *Cyclops* Muller

Cyclops vernalis was taken from all drainages, at all seasons and from all types of habitats. It is quite variable, especially in the spination of the fourth swimming legs and the length of the spines of the fifth legs. Although collected during all seasons, *C. vernalis* was most abundant during the winter and early spring periods.

C. bicuspidatus thomasi was one of the most abundant cyclopoid species in the early winter and spring collections, but was not taken during the summer. It occurred in all drainages except the Tombigbee and in all types of habitats. Of the 27 collections made of this species, 17 were from lakes and ponds.

C. crassicaudis brachycercus was collected only in offshore plankton tows from two large impoundments in the Yazoo drainage.

C. varicans rubellus is a small, obscure species that was widespread but not common. It was taken from all habitats with the exception of ponds, and in all seasons. *C. v. rubellus* was found in all drainages except the area immediately adjacent to the Mississippi River.

Genus *Mesocyclops* Sars

Mesocyclops edax was present throughout the year and was widespread during the early spring collection. It was found in all habitats and all drainages with the exception of the Tennessee.

M. tenuis is a rare species that was taken once during the late summer of 1972 in a large oxbow lake between the levee and the Mississippi River in northwestern Mississippi.

Genus *Macrocyclops* Claus

Macrocyclops fuscus was found and identified only once from an immature form

collected during the late summer of 1972 in a small lake in the Tombigbee River drainage.

M. albidus was a common species widespread throughout the year in all habitats and all drainage systems except that of the Mississippi River proper.

M. ater is a widespread but uncommon form in the United States. It was collected once during the early spring in the Yazoo drainage in about 0.3 m of water in a flooded field adjacent to a farm pond, but was never taken from the pond itself.

DISCUSSION

During the course of the investigation, several significant range extensions were uncovered. *Eurytomora affinis* is a euryhaline species that is usually found in lakes and ponds of coastal areas (Wilson & Yeatman, 1959); however, during the current investigation specimens were recovered 1145 km upriver from the Gulf of Mexico well beyond any saltwater intrusion. Either this species has been missed in previous freshwater collections, or it is currently migrating into the inland freshwater environment. *Mesocyclops tenuis* is a rare species that has been collected primarily in the southwestern United States but was taken once during the summer of 1972 in northwestern Mississippi. *Cyclops crassicaudis brachycercus,* according to Bunting (1973), has previously been taken only from stagnant, temporary pools and wells and from littoral areas of shallow lakes. In northern Mississippi it was taken only in offshore plankton tows in two large man-made reservoirs. With more thorough collecting, many of these species with restricted ranges will undoubtedly prove to be more widely distributed than once thought.

A number of problems arose during this investigation concerning the interpretation of several species-subspecies complexes. Females of *Diaptomus pallidus* and *D. reighardi* posed one of the most difficult problems of the survey. The chief distinguishing charateristic between the two is the length of the two lateral setae of the terminal exopod segment of the fifth legs. In *D. reighardi* the inner seta is longer and reaches beyond the middle of the claw, while in *D. pallidus,* the two setae are nearly equal in length and do not reach beyond the middle of the claw. A large number of individuals were encountered during this study that were transitional between the two species. Until a detailed investigation of the differences between them can be compeleted, identification of females of these species should be made with caution.

Another problem concerns the *Eucyclops agilis-E. speratus* relationship. From the material collected in northern Mississippi, there seems to be no easily recognizable distinction between them. Supposedly the main differences between the two are relative length of the caudal rami, length of the inner corner setae of the caudal rami and the prominence of the lateral spinules on the caudal rami. In the study area numerous individuals were found with characters intermediate between these species. Many individuals with the long caudal rami of *E. speratus* also had prominent lateral spinules of the caudal rami characteristic of *E. agilis.*

Tropocyclops prasinus and *T. p. mexicanus* presented another area of concern. Distribution notes by Wilson & Yeatman (1959) indicate that *T. prasinus* is the common form, but in northern Mississippi *T. p. mexicanus* is prevalent. Although, as expected, many individuals appeared intermediate between these two groups, the fact that *T. p. mexicanus, T. prasinus* and intermediates were taken from the same body of water at the same time indicates a need for reviewing the validity of this species/subspecies complex. Two other species were represented by two subspecies in the study area: *Eucyclops agilis* and *E. agilis montanus* and *Paracyclops fimbriatus* and *P. fimbriatus poppei.* Neither of these couples were collected from any body of water at the same time although they did occur in the same waters at different seasons. Further investigations of these subspecies is needed to determine if they are truly different or merely seasonal variations.

Of the calanoid copepods *D. pallidus* was the most common and widespread during all

seasons and the most common and widespread copepod collected during the summer period. *T. prasinus* and *T. p. mexicanus* were by far the most widely distributed cyclopoid copepods in the late summer, winter and early summer collections and were second only to *Eucyclops agilis* in the early spring collections. *T. p. mexicanus* was the most widespread copepod during the winter collection with *D. pallidus* being second.

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EVOLUTION AND FOSSIL RECORD OF THE CHICKEN TURTLE *DEIROCHELYS*, WITH A RE-EVALUATION OF THE GENUS

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ABSTRACT

Prior evidence of the fossil history of the monotypic genus *Deirochelys* is limited to a single upper Pleistocene fragment and a number of sub-Recent elements from Florida. On the basis of several morphological adaptions unusual among emydine turtles (e.g., neural bone width and rib structure), fossils from 20 Florida sites, ranging from Miocene to sub-Recent in age, are referred to the genus *Deirochelys*. Evidence of the gradual evolution of a specialized suite of characters associated with pharyngeal feeding is presented. The middle Pliocene representative of the genus is recognized as a distinct species *(Deirochelys carri,* sp. nov.) intermediate between Recent *D. reticularia* and less specialized emydines such as *Chrysemys*. *Deirochelys* fossils from the Thomas Farm Miocene are more primitive than *D. carri* and further bridge the morphological gap between *Chrysemys* and *Deirochelys*.

The evolutionary history of the monotypic genus *Deirochelys* is one of the more enigmatic chapters in our knowledge of North American emydid turtles. Previous workers (Carr, 1952; Loveridge and Williams, 1957; McDowell, 1964) have generally agreed that *Deirochelys* is a highly specialized derivative of the genus *Chrysemys* (sensu McDowell, 1964). Furthermore, Baur's (1889) suggestion of a close phylogenetic relationship between *Deirochelys* and another North American monotypic emydine genus, *Emydoidea,* has been supported by most subsequent workers Loveridge and Williams, 1957; C. Jackson, 1959; McDowell, 1964; Zug and Schwartz, 1971). Recently Waagen (1972) and Bramble (1974) have cast doubt on this idea based on their respective studies of musk glands and shell mechanics.

The fossil record has been of no help in these matters to date. Prior knowledge of the fossil history of the genus *Deirochelys* is limited to description of one partial nuchal bone from the upper Pleistocene of Florida (C. Jackson, 1964, 1974a) and to mention of the presence of *D. reticularia* in a sub-Recent Florida site (Hirschfeld, 1968). Crawford Jackson (1964) found that the Pleistocene element represents a turtle conspecific with Recent *D. reticularia.* All other fossils previously assigned to the genus, i.e., *Deirochelys floridana* Hay and *Trachemys jarmani* Hay (Hay, 1908; Weaver and Robertson, 1967), actually represent the genus *Chrysemys* (C. Jackson, 1964, 1974a).

This paper examines material referable to the genus *Deirochelys* from one Miocene, five Pliocene, 12 Pleistocene, and two sub-Recent sites, all in Florida. The Miocene fossils are the oldest known representatives of the genus. Two species of *Deirochelys,* one new, are recognized as fossils. As will be shown the major course of evolution within *Deirochelys* has been the extreme elongation of the head and neck, a condition achieved by only one other emydine genus *(Emydoidea)* and presumably developed as a trophic specialization. The accompanying cervical musculature hypertrophy has necessitated further structural modifications of the shell and vertebral column. It is for this reason that in tracing the evolution of the genus I dwell primarily upon this cervicocranial elongation and associated morphological modifications (e.g., changes in neural bone width and rib and vertebral structures),

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to which I collectively refer hereafter as a single "character suite."

MATERIALS AND METHODS

All fossil specimens except those from Waccasassa River and a few from Thomas Farm are part of the vertebrate paleontology collection of the Florida State Museum (UF); the Waccasassa River I specimens are from the Timberlane Research Organization (TRO),
the Thomas Farm fossils are from the collections of the Museum of Comparative Zoology, Harvard University (MCZ). Comparative skeletal material was examined from the herpetology collection of the Florida State Museum (UF), the National Museum of Natural History (USNM), and my personal collection (DRJ). Extant specimens examined were *Deirochelys reticularia:* DRJ 264, 266, 270, 274, 278-280, 300, UF 1420, 7744, 14244, USNM 11610, 11615, 29477, 29584, 62219, 80965, 95789; *Emydoidea blandingii:* UF 14249, 18931; *Chelydra serpentina:* DRJ 253; *Chelus fimbriata:* UF 21977.

A shell thickness index (STI) was determined for most fossils. Thicknesses of fossil shell elements were measured and divided by corresponding measurements of a series ($N = 10$) of Recent adult *D. reticularia* of corresponding size, or by linear extrapolations to approximate such if a Recent specimen of sufficient size were unavailable. As the relationship between shell thickness and body length may not be strictly linear, the STI values given for the largest fossils may actually be underestimates. There was little individual STI variation among the Recent specimens when corrected for differences in body length. More medial elements (neural bones and proximal ends of pleural bones) generally yielded slightly higher STI values than peripheral elements (peripheral, pygal, and nuchal bones), indicating that increase in shell thickness is not necessarily proportional for all parts of the same shell. Medial edges of peripheral elements were measured to reduce this discrepancy.

An index of free rib length (width of rib canal) was determined by dividing the straight-line distance from the proximal tip of the pleural bone to its union with the rib by the width of the pleural bone at the level of the union. The fragmented condition of most of the fossils necessitated the use of pleural bone width rather than length.

In comparing neural and pleural bones of fossil *Deirochelys* with those of Recent specimens, it is necessary to determine which of the eight neural or pleural bones the fossils represent. The presence and position of scute sulci as well as the relative proportions of the anterolateral and posterolateral borders of the bones usually make this possible. Because of the relatively great width and frequent anomalies of the posterior neural bones of most emydine turtles, these bones are of little taxonomic value.

All measurements are maximum and given in millimeters.

FOSSIL LOCALITIES

The Appendix provides an annotated list of Florida localities that have yielded fossil *Deirochelys* mentioned in this paper. Reference is made to other publications in which stratigraphy, paleoecology, and correlative age of each of these deposits is described in detail. Figure 1 shows the geographic distribution of these sites.

SYSTEMATIC DESCRIPTIONS

All past descriptions of the genus *Deirochelys* (Agassiz, 1857; Baur, 1889; White, 1929; Schwartz, 1956; C. Jackson, 1959; McDowell, 1964; Zug and Schwartz, 1971) have necessarily been drawn solely from the single extant species, *D. reticularia.* Hence, many characters which would have been more appropriately designated as specific characters, particularly those involving color pattern, have been incorporated into the definition of the genus. Therefore, in order to accommodate the fossil members of the genus it is necessary to relegate many of the generic characters, including all references to color pattern, to specific level. Additionally, an examination of osteological characters

through time reveals phylogenetic changes within the genus that may be used to distinguish certain allochronic forms. For these reasons I find it necessary to give a brief systematic reevaluation of the genus as a prelude to a formal description of the fossil forms. The present chronologically-expanded definition of the genus, like those of Baur (1889), White (1929), C. Jackson (1959) and McDowell (1964), is based solely on osteological characters. As fossil skull material is presently unknown, all skull characters are drawn from Recent *D. reticularia*. Schwartz (1957) gives a brief but adequate account of the taxonomic history of the genus.

Family Emydidae
Subfamily Emydinae
Genus *Deirochelys* Agassiz

To the generic synonymy given by Zug and Schwartz (1971) should be added the following entry:

Hirochelys Beyer, 1900: 45.

Type. Testudo reticularia Latreille.

Referred species. Deirochelys reticularia, the only extant species, at present distributed throughout the southeastern United States and known from the Pleistocene of Florida; *Deirochelys carri,* new species, middle Pliocene Alachua clays of Florida, Hemphillian age.

Definition. Shell elongate to subovate in adults; carapace elliptical or cuneiform in outline and usually sculptured with fine parallel ridges or scales (Fig. 2); anterior edge of nuchal bone generally truncate and acuminate; lateral sulci of nuchal scute usually parallel above and below; nuchal scute usually two to three times longer than wide above, approximately as wide as long below; nuchal bone overlapped by only small corner of first coastal scute or not at all; vertebral scutes as wide as long; neural bones hexagonal, short-sided in front; first neural bone circular to subovate in outline; other neural bones generally as wide or wider than long (Fig. 2); peripheral bones unnotched; pygal bone approximately parallel-sided with a shallow mesial notch; ribs dorsally free from pleural bones well below proximal ends of pleurals, their free portions slender and bowed ventrally (Fig. 3) accommodating the enlarged trunk vertebral muscle complex (Shah, 1963).

Plastron usually considerably narrower than carapace, akinetic, and firmly united to carapace by a high bony bridge and plastral buttresses; inguinal scutes large (contrary to

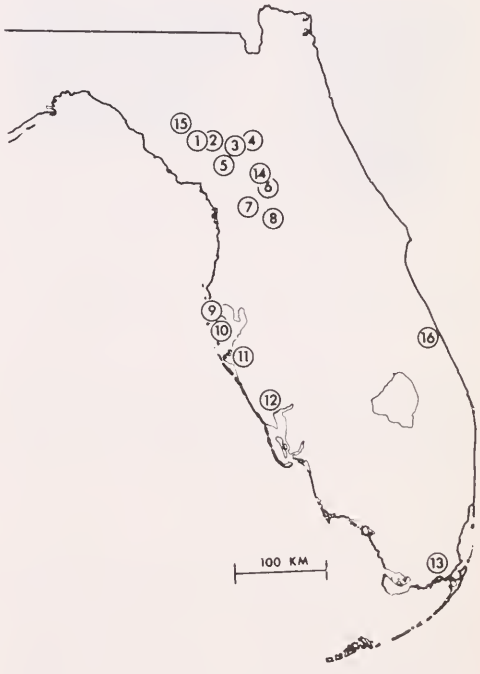

Fig. 1. Fossil sites in peninsular Florida containing *Deirochelys*. Site ages are given in Appendix.

1. McGehee Farm
2. Haile sites
3. Love Bone Bed
4. Wall Company Pit
5. Mixson's Bone Bed
6. Kendrick IA
7. Waccasassa River sites
8. Coleman IIIC
9. Seminole Field
10. Catalina Gardens
11. Bradenton
12. Warm Mineral Springs
13. Nichol's Hammock

Holman's [1967] statement that they are absent); plastron smooth ventrally or with traces of sculpturing similar to but less pronounced than that of carapace; entoplastron usually anterior to humeropectoral sulcus and overlapped by gular scutes for approximately one third of length.

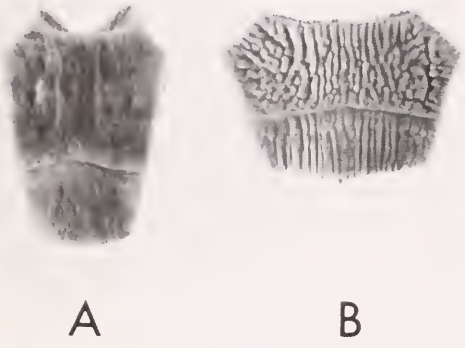

Fig. 2. Third neural bones of *Chrysemys floridana* (A) and *Deirochelys reticularia* (B); note greater width and characteristic sculpturing of latter.

Skull and second through seventh cervical vertebrae elongate; neural spines of anterior thoracic vertebrae laterally compressed as vertical sheets (Fig. 4); triturating surfaces of maxilla and mandible narrow, without ridges; beak never hooked; interorbital width very narrow, less than one-half diameter of orbit; palate decidedly flat; posterior palatine foramina much larger than foramina orbito-nasale (Gaffney, 1972) [= anterior palatine foramina of Hoffman, 1890]; temporal arcade complete; quadrate nearly enclosing stapes; coronoid relatively low; hyoid apparatus strongly developed, lateral horn length at least as great as skull width; cervical musculature as described by Shah (1963).

A specialization of the genus almost certainly related to the elongate neck and hypertrophied vertebral musculature is the modification of the spinal column. The differences between *Deirochelys* and more primitive emydines (e.g., *Chrysemys),* summarized in Table 1 and Fig. 4, are most conspicuous in the first four thoracic vertebrae. In both forms ribs attach intercentrally and the thoracic vertebrae are united by their neural spines to the overlying neural bones. The net effect of these modifications in *Deirochelys* has been to move the rib attachment ventrally (away from the carapace), allowing for the hypertrophied trunk vertebral musculature without changing the distance of the spinal cord from the ventral surface of the carapace.

Deirochelys reticularia (Latreille)
Chicken turtle

The only addition to the species synonymy listed by Zug and Schwartz (1971) is:

Hirochelys reticulata Beyer, 1900:45.

Type: The type was formerly in the collection of the French Museum National d'Histoire Naturelle but is now considered lost (Schwartz, 1956). Schwartz (1956) described a neotype and neoallotype from the vicinity of the original type locality.

Type locality. Restricted by Harper (1940) to the vicinity of Charleston, South Carolina.

Diagnosis: A *Deirochelys* characterized by relatively low length: width ratios for third through fifth neural bones (means, 0.6 to 0.7; Fig. 5) and relatively great length of free portions of dorsal ribs (Fig. 6); coloration as described by Schwartz (1956) with notation that the yellow forelimb band is

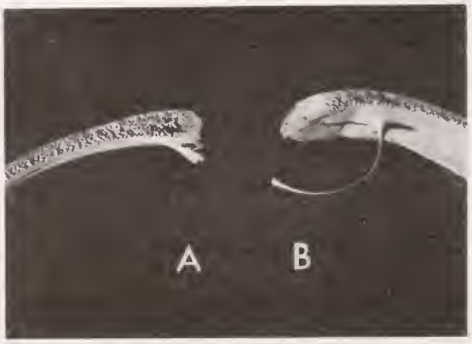

Fig. 3. Frontal aspects of third pleural bones of *Chrysemys concinna* (A) and *Deirochelys reticularia* (B), showing dorsal ribs.

Table 1. Comparison of the thoracic vertebrae of *Deirochelys* and *Chrysemys*.

Character	*Chrysemys*	*Deirochelys*
Neural spines	low and robust	laterally compressed as vertical sheets
Centra	narrowest ventrally; not compressed	narrowest dorsally; dorsoventrally compressed; ventral surfaces wide and flattened
Site of rib attachment to veter	expanded dorsal region of centra	expanded ventral region of centra

usually but not always wide; neck nearly as long as plastron; usual pattern of cervical central articulation (perhaps a generic character): (2((3((4))5))6))7((8) (Williams, 1950; C. Jackson, 1974b).

Description of fossil material. The following fossils, listed in reversed chronologic order by site, are here assigned to *D. reticularia.*

Nichol's Hammock: contains more *D. reticularia* than any other post-Pliocene site; 75 carapacial elements (UF 20892), a cervical vertebra (UF 20904), and a supraoccipital crest (UF 20905) represent 12 to 20 individuals ranging from 65 mm to 195mm carapace length (CL); many additional elements from this deposit, particularly plastral and peripheral bones which lack diagnostic features, probably represent *D. reticularia* as well; fossils from the site are indistinguishable from extant *D. reticularia,* their shallow rugosity probably reflecting their relatively small size; STI 0.95 to 1.05.

Warm Mineral Springs: To date, 35 elements – one nuchal, seven neural, one suprapygal, six pleural, 13 peripheral, and five plastral bones, plus a scapula and broken femur – all assigned field number WMS 19352 and representing 5 to 10 individuals of CL 138 to 184, have been removed from this site. The bones are similar to those from Nichol's Hammock and have an average STI of 1.15.

Vero: A large number of plastral and carapacial elements, including at least two nuchal, two neural and two pleural bones (all recently acquired by the Florida State Museum as part of the former Florida Geological Survey ,collection and as yet uncatalogued) are virtually indistinguishable from modern *D. reticularia;* STI 0.85-0.95.

Waccasassa River I: Two second neural bones (TRO 101, 102) and a third neural bone (TRO 103), representing three individuals of 130 to 210 CL (Fig. 7); STI 1.1 to 1.3.

Waccasassa River V: A lightly-sculptured nuchal bone, UF 16271 (Fig. 7): greatest length 30.5, greatest width 35.5, estimated CL 135; proximal end of a pleural bone, UF 16275; STI 1.1.

Waccasassa River VI: A distinctly grooved nuchal bone, UF 21906: greatest length 39.8, greatest width 42.3, estimated CL 170; STI 1.1.

Reddick IIC: A first neural bone (UF 21955) from an adult turtle (estimated CL 180) and the proximal end of a fourth pleural bone from a juvenile; STI 1.1.

Coleman IIIC: Four elements (UF 15186E) representing at least three individuals: a longitudinally rugose, relatively deeply notched pygal bone (length 21.5); a left epiplastron (interepiplastral suture length 13.6); a characteristically rugose left xiphiplastron missing its distal portion (hypo-xiphiplastral suture length 40.7); and a distinctly sculptured right hypoplastron (interhypoplastral suture length 58.4); STI 1.3.

St. Petersburg, Catalina Gardens: Lower two thirds of a right fifth pleural bone (UF 19248): greatest width 30.0, estimated length 60, estimated CL 220; STI 1.3.

Seminole Field: A deeply sculptured fragment of a right second pleural bone (UF 9927) with rib attachment – width at rib level 28.0, thickness at rib level 5.9, estimated CL 210; fragment of a left hypoplastron (UF 9927) with deep longitudinal grooves on ventral surface, estimated CL 210; STI 1.4.

Bradenton 51st Street: A characteristically

sculptured fragment of a nuchal bone (UF 2482): estimated CL 210, STI 1.25.

Kendrick IA: A sixth neural bone (UF 19250) with a pronounced, scale-like sculpturing and a low, rounded keel – greatest length 19.3, greatest width 33.2, greatest thickness 6.0, estimated CL 250, STI 1.3; a deeply grooved partial nuchal bone (UF 9292) possibly from the same individual and described previously by C. Jackson (1964): estimated CL 250, STI 1.1 to 1.6; (Fig. 8).

Wall Company Pit: Proximal halves of two broken pleural bones (UF 5026): a second left (estimated CL 175, STI 1.6) and a deeply rugose fourth right (estimated CL 220, STI 1.5) with rib distance: pleural width ratios of 0.84 and 0.80, respectively.

Haile XVI: 38 elements representing at least 15 individuals of CL 116 to 240: a nuchal bone (UF 20896), length 40.0, estimated CL 182; a second neural bone contiguous with the second and third right pleural bones (UF 20888; Fig. 9), and the first left and second right peripheral bones (UF 20889) almost certainly from the same individual, estimated CL 230; fifteen fragmentary pleural bones (UF 20895; UF 20898) and seven peripheral bones (UF 21970); a hypoplastron (UF 21969) and partial hypoplastron (UF 21968); second left pleural bone and first four neural bones (UF 20893) from a turtle of 227 CL; and the third (UF 20897), fourth (UF 21971), two fifth (UF 20894 and UF 20898), and sixth (UF 20898) neural bones from five turtles with CL of 240, 140, 225, 160 and 220, respectively. Neural length: width and rib distance: pleural width ratios are included in Figs. 5 and 6; STI of neural bones 2.0 to 2.2.

Haile XVA: A fifth neural bone (UF 19249), the dorsal surface of which is extremely flat but moderately sculptured: greatest length

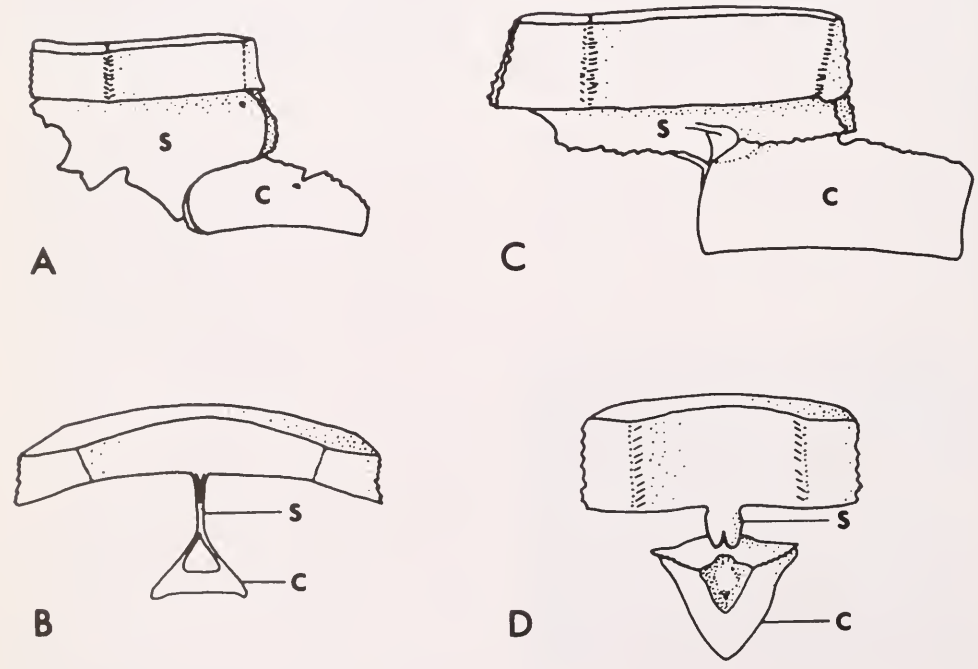

Fig. 4. Lateral (A, C) and frontal (B, D) aspects of third neural bones and associated vertebrae of *Deirochelys reticularia* (A,B) and *Chrysemys nelsoni* (C, D); c, centrum; s, neural spine.

20.2, greatest width 32.0, estimated CL 210; an anterior fragment of a nuchal bone (UF 19168), estimated CL 230; STI 1.5; (Fig. 10).

Discussion of fossil material. All of the Rancholabrean and sub-Recent material is clearly referable to *D. reticularia*. With the exception of shell thickness, relative dimensions of individual fossils show no significant differences from corresponding measurements of extant turtles. The Blancan and Irvingtonian material, as well as the Kendrick nuchal, indicate that this species reached a slightly larger maximum size during the Late Pliocene and Pleistocene than at present. The blunt median keel on the Kendrick neural, although not typical of most extant *D. reticularia*, occurs posteriorly in a

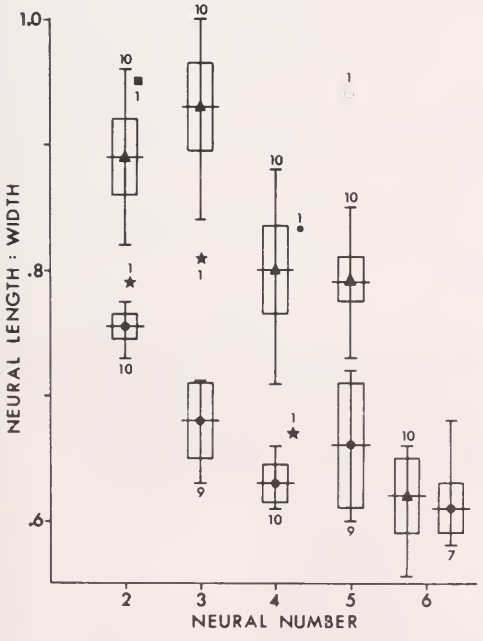

Fig. 5. Length: width ratios of second through sixth neural bones of Recent (circles), Irvingtonian (stars) and Hemphillian (triangles – Love; square – Haile VI; asterisk – Mixson's) *Deirochelys*. Dice – Leraas diagrams depict mean, range, and two standard errors; numbers above and below bars represent sample sizes.

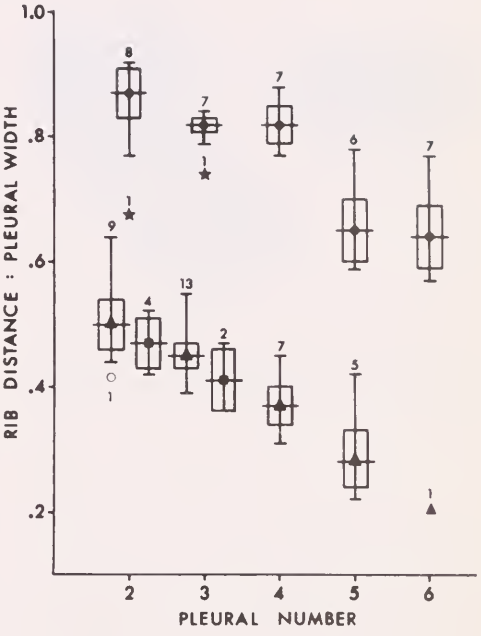

Fig. 6. Rib distance: pleural bone width ratios for Recent, Pleistocene, and Pliocene (*Deirochelys;* all symbols as in Fig. 5.

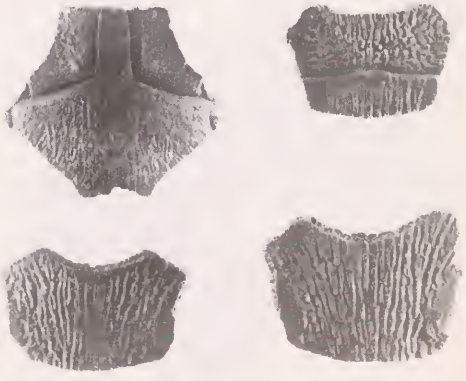

Fig. 7. Nuchal bone (UF 16271) and three neural bones (TRO 101-103) of Rancholabrean *Deirochelys reticularia* from Waccasassa River VA and I, respectively.

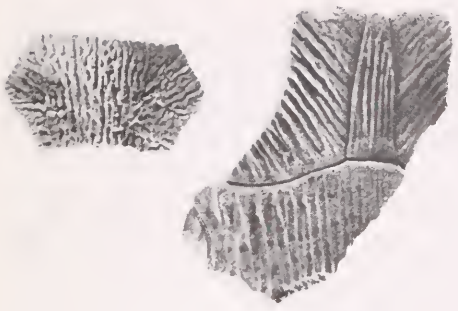

Fig. 8. Distinctly sculptured sixth neural bone (UF 19250) of *Deirochelys reticularia* from Kendrick IA.

few individuals. Though tending to be more pronounced in the Pleistocene, shell rugosity patterns are within the range of variation of extant *D. reticularia*.

The single consistent difference between Pleistocene and Recent *D. reticularia* is that of shell thickness. The STI of Pleistocene *D. reticularia* is 1.1 to 2.2 times that of Recent specimens. The trend towards shell thickness reduction appears roughly chronoclinal since at least the Irvingtonian (Table 2), though the absence of material from some glacial and interglacial periods may conceal unseen fluctuations. Similar trends in post-Pliocene shell thickness reduction have been suggested, though less well supported by a time-transgressive series of fossils, for *Chrysemys* (Preston, 1966, 1971), *Emydoidea* (Taylor, 1943), *Graptemys* (D. Jackson, 1975), *Kinosternon* (Fichter, 1969), *Trionyx* (Wood and Patterson, 1973) and *Geochelone* (Auffenberg, 1963b). Although shell thickness alone is inadequate as a basis for taxonomic separation, it is not a simple function of turtle size as Auffenberg (1958) states for *Terrapene*. From middle Pleistocene to the present, the shell of *D. reticularia* has become progressively thinner. Gaps in the STI-time curve may reflect our incomplete sampling of the fossil record. Nevertheless, the possibility of sexual and ontogenetic polymorphism in this character, as well as hidden fluctuations in the curve, could complicate the matter. Unfortunately, sample sizes from most fossil sites are inadequate for a thorough treatment of the data.

The Irvingtonian (Haile XVI) fossils differ from younger material in two additional ways: a higher length: width ratio for the second and third neural bones (Fig. 5) and a slightly more proximal site of rib juncture with the second and third pleural bones (Fig. 6). These characters do not exhibit allome-

Fig. 9. Dorsal (A) and ventral (B) views of part of carapace (UF 20888) of Irvingtonian *Deirochelys reticularia* from Haile XVI. Note characteristic sculpturing, neural bone width, and rib junctures.

Table 2. Shell thickness index (STI) of fossil *Deirochelys* from 16 Florida sites listed chronologically by faunal periods.

Age and Site	STI
Hemingfordian	
Thomas Farm	1.9
Hemphillian	
Love	1.6-2.1
Mixson	1.8
Haile VI	1.9
Blancan	
Haile XV	1.5
Irvingtonian	
Haile XVI	2.0-2.2
Rancholabrean	
Wall Co. Pit	1.5-1.6
Bradenton	1.25
Kendrick	1.3
Seminole Field	1.4
Catalina Gardens	1.3
Coleman IIIC	1.3
Waccasassa I	1.1-1.3
Waccasassa V	1.1
Sub-Recent	
Warm Mineral Spring	1.15
Nichol's Hammock	0.95-1.05

try in Recent adult specimens, and there is thus no reason to suspect it in Pleistocene populations. In these respects Irvingtonian *Deirochelys* are morphologically intermediate between the later Pleistocene and the middle Pliocene turtles discussed below. The near identity of the Blancan neural (UF 19249) with that of an Irvingtonian one (UF 20894) suggests that little shell evolution was experienced between these periods.

The differences between Recent and upper Pliocene to middle Pleistocene *Deirochelys* are real and might justify taxonomic distinction were it not for the intermediate Rancholabrean material. Such time-related changes are, however, to be expected within a chronoclinal lineage, as shown previously by Milstead (1967) with *Terrapene*. The modern subspecies of *D. reticularia* are distinguished by coloration and shell shape (Schwartz, 1956) and consequently can not be compared to these fossils. Furthermore, *D. reticularia* likely varied geographically during the Pleistocene as it does now. For these reasons I refrain from erecting subspecific epithets for any of the Pleistocene or upper Pliocene fossils and simply refer them all to the species *Deirochelys reticularia*.

The existence of certain morphological differences, reflected in carapacial osteology, of specimens referred above to *D. reticularia* and all earlier representatives of the genus (Figs. 5 and 6) is accentuated by the absence of late Hemphillian fossils. This gap in a gradually evolving lineage creates a convenient (though admittedly artificial) point of division between morphologically distinct forms. I therefore designate the turtle represented by the middle Pliocene fossils as

Deirochelys carri, new species

Etymology. Named in honor of Archie F. Carr, Jr. for his extensive contributions to our knowledge of Recent turtles and to herpetology in general.

Holotype. UF 20908, a fragmented but nearly complete carapace lacking only the nuchal bone, first neural bone, and anterior peripheral bones (Fig. 11A); a partial plastron consisting of the left hyoplastron, hypoplastron, and xiphiplastron apparently represents the same individual (Fig. 11B).

Type locality and horizon. Alachua Clay, Love Bone Bed, near Archer, Alachua County, Florida; early Hemphillian, middle Pliocene.

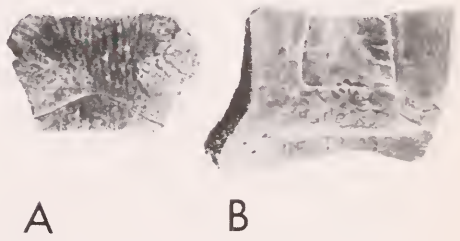

Fig. 10. Blancan *Deirochelys reticularia* from Haile XVA; (A) fifth neural bone (UF 19249) and (B) nuchal bone fragment (UF 19168) showing broad nuchal scute underlap.

Referred material. All from four Florida sites producing Hemphillian faunas:

Mixson's Bone Bed: a fourth neural bone, UF 20890 (formerly Florida Geological Survey V-2599), assigned previously by Hay (1916) to *Chrysemys caelata:* estimated CL 290, STI 1.8.

McGehee Farm: a complete (UF 19204) and two partial (UF 20891 and UF 20903) nuchal bones – measurements of UF 19204: length 57.1, width 60.8, corresponding to a CL of approximately 263; right hypoplastron, ninth right peripheral bone, and left and right xiphiplastral fragments (UF 20899).

Haile VI: contiguous second neural bone fragment and proximal portion of left second pleural bone (UF 20887); estimated CL 253, STI 1.9; contiguous pygal bone and eleventh left peripheral bone (UF 6485a); anterior end of third cervical vertebra (lacking zygapophyses) (UF 6485b , Fig. 12); five peripheral bones UF (6485c); first neural bone, (UF 6485d); 17 pleural bone fragments (UF 6485e); many other elements and fragments from this site may represent either *D. carri* or *Chrysemys caelata* (D. Jackson, 1976).

Love Bone Bed: Although excavation is incomplete, this deposit is already the richest source of fossil *Deirochelys* known. At the time of this writing over 400 carapacial elements and half as many plastral elements of *Deirochelys* have been removed. Other than the holotype, only two sets of associated carapacial bones have been found (UF 24100 and UF 20900, Fig. 13). The less water-worn carapacial elements display the distinct scale-like sculpturing characteristic of the genus (Fig. 14). Many elements represent turtles of exceptionally large size for *Deirochelys:* the largest nuchal bone (UF

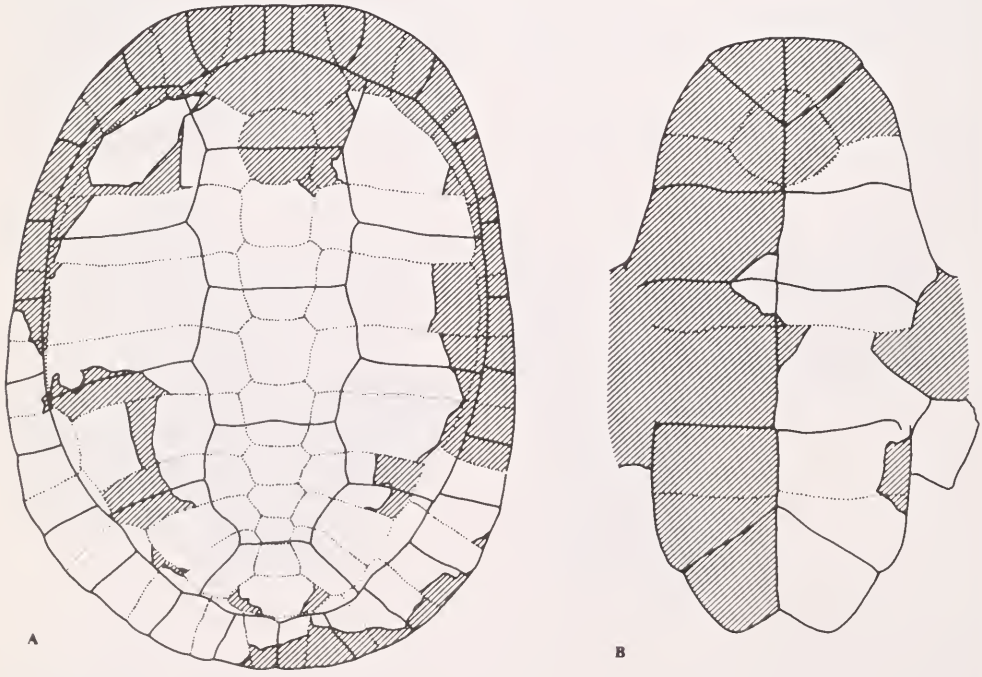

Fig. 11. *Deirochelys carri* holotype, UF 20908. (A) Dorsal aspect of carapace; (B) Ventral aspect of plastron. Hatched areas missing from fossil.

20906) measures 59.8 (length) x 61.8 (width). STI range is 1.6 to 2.1.

Diagnosis. Deirochelys carri differs from *D. reticularia* in having relatively narrower neural bones (mean length: width ratio of third through fifth neural bones 0.8 to 0.9; Figs. 5, 11A) and a more proximal site of emergence of the ribs from the pleural bones (Figs. 6, 13). Elongation of cervical vertebrae and patterns of shell rugosity are similar in these species, but the carapace of *D. carri* appears to be relatively broader.

Shell rugosity and width of first vertebral scute of *D. carri* are like those of *Chrysemys caelata* and *C. williamsi,* respectively, also from the Florida Pliocene (D. Jackson, 1976); nevertheless, other generic characters distinguish these species from *D. carri.* Neural bones of *D. carri* are similar in shape to those of the Florida Pliocene *Chrysemys inflata* (Weaver and Robertson, 1967), yet distinguished from them by absence of the pronounced keel and deeply excavated surface of the latter.

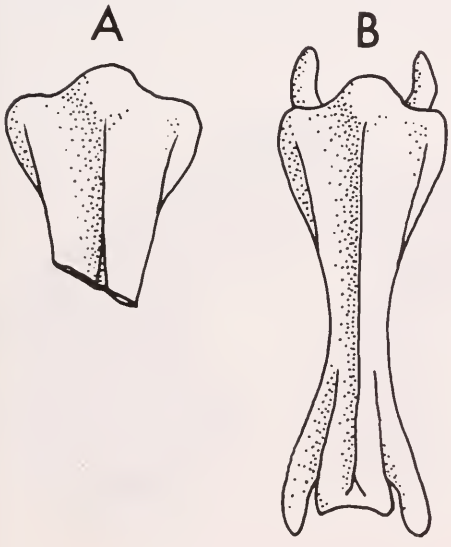

Fig. 12. Ventral surfaces of third cervical vertebrae of (A) *Deirochelys carri* (UF 64856) and (B) *D. reticularia* (DRJ 300) (x2.2).

Description. With the exception of the less developed character suite previously alluded to, *D. carri* is, in most respects, similar to *D. reticularia.* Nevertheless, many of the fossils indicate that the former reached a greater size than *D. reticularia,* perhaps as large as 320 mm CL compared to approximately 250 mm CL today (Carr, 1952). The shell of *D. carri* is about twice as thick as that of extant *D. reticularia* but not unlike that of Blancan and Irvingtonian representatives of the modern species (Table 2). Additionally, the reconstructed holotype shell is relatively broad and flat compared to Recent chicken turtles. In this respect, as well as in the flaring of the posterior peripheral bones, *D. carri* is reminiscent of some members of the genus *Chrysemys* and appears to have been more streamlined than *D. reticularia.* One fairly constant difference between *D. reticularia* and *D. carri* is that the anterior edge of the fourth vertebral scute (incised at the fifth neural bone) of *D. reticularia* projects forward to form a sharp anteriorly-directed V, whereas that of *D. carri* projects forward only slightly (and more bluntly) or not at all (Fig. 11A). The plastron of *D. carri,* like that of *D. reticularia,* is narrow. The anal notch in the plastron associated with the holotype of *D. carri* is twice as deep as that of *D. reticularia.* There is no significant morphological variation among *D. carri* from the four sites. Measurements and qualitative observations of all material from Haile VI, McGehee Farm, and Mixson's Bone Bed fall within the range of variation of elements from the Love Bone Bed.

Comment. Deirochelys carri is similar in most respects to its presumed descendant *D. reticularia.* The major differences are modifications associated with the further development of the specialized elongate neck and head in *D. reticularia.* In this respect both *D. carri* and *D. reticularia* surely represent segments of a single chronoclinal lineage. The neural spines and dorsal rib heads of *D. carri* are typical of the genus and only slightly more robust than those of *D. reticularia.* The single cervical vertebra (UF 6485b) referable

to *D. carri* is likewise slightly more robust than the corresponding vertebra of *D. reticularia* (Fig. 12). Although it is impossible to determine accurately the length of the Pliocene vertebra from the Haile VI fragment, it appears that the characteristic cervical elongation and development of associated modifications in *Deirochelys* had already approached present levels by middle Pliocene. Nevertheless, the narrower neural bones and more proximal rib union with the pleural bones in *D. carri,* compared with *D. reticularia,* imply a shorter free rib between the pleurals and vertebral column and a correspondingly less developed set of cervical extensor muscles in the former. A slightly shorter or less powerful neck in the Pliocene species therefore seems likely. Certainly any future finds of *Deirochelys* skull and cervical material in the Love Bone Bed would be particularly valuable.

Although the Love Bone Bed provides an exceptionally fine series of *Deirochelys* fossils, far older than any previously known for the genus, one can trace the evolutionary record back one step further – to the Miocene.

The Thomas Farm *Deirochelys*

The only emydine turtle previously recognized from the Florida Miocene (Thomas Farm) is a *Chrysemys* species of uncertain status (Williams, 1953; Rose and Weaver, 1966). In an effort to determine the relationships of this turtle, I examined the holdings of the Florida State Museum for additional material. Among the elements retrieved were a faintly sculptured neural bone (UF 21949) only slightly narrower than those of *Deirochelys carri,* and the proximal fragment of a pleural bone (UF 21950) with a rib juncture scar too low for that of *Chrysemys* (Fig. 15). Comparisons with Recent and fossil *Deirochelys* and *Chrysemys,* including "typical" *Chrysemys* elements from Thomas Farm, leave no doubt that the two fossils represent *Deirochelys.* Curvature of the scute sulcus, relative length of the anterolateral borders, and extreme lowness of the neural spine all indicate that the neural bone is a fifth, while the relative proportions of the medial borders of the pleural bone in addition to the position of the sulcus indicate that it probably is the second pleural bone from the left side. As

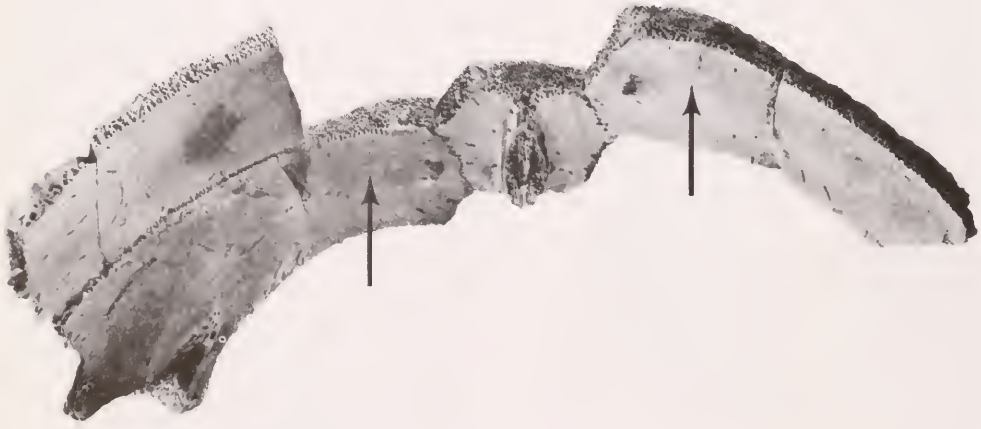

Fig. 13. Ventral surface of posterior region of *Deirochelys carri* carapace, UF 20900, showing rib juncture with pleural bones. Arrows indicate where junctures would occur in a *D. reticularia* of equivalent size.

with the Pliocene *Deirochelys,* the shell is relatively thick (STI 1.9).

In addition to the two fossils described above, I tentatively refer to *Deirochelys* the following elements from Thomas Farm: one complete epiplastron (UF 21932) and the medial half of another (UF 21939), the posterior part of a right xiphiplastron (UF 21946), the major part of an entoplastron (UF 21942), and the proximal end of a pleural bone (UF 21951). Additionally, one complete and two fragmentary nuchal bones (MCZ 3432; see Fig. 4 in Williams, 1953, and Fig. 2B in Rose and Weaver, 1966), although probably representing *Chrysemys,* may be *Deirochelys.* The width of the first vertebral scute and shape of the nuchal scute are like those of both *Deirochelys* and *Chrysemys ornata.*

Both the shape of the neural bone (length: width ratio, 0.94, Fig. 5) and the point of juncture of the rib with the pleural bone (rib distance: pleural bone width ratio, 0.41, Fig. 6) indicate that, in terms of cervical hypertrophy, the Thomas Farm *Deirochelys* was even more primitive (less specialized) than *D. carri.* Remains of the very low neural spine fused to the neural bone confirm this. Hence, I believe that the limited Thomas Farm material represents a turtle distinct from *D. carri.* However, any taxonomic assignment of the Thomas Farm fossils other than to genus must await additional and preferably associated material. More important at present is that in the Thomas Farm Miocene we find an important link in the gradual evolutionary sequence from a generalized emydine ancestor (cf. *Chrysemys*) into the more specialized *D. carri* and its highly specialized descendant, *D. reticularia.*

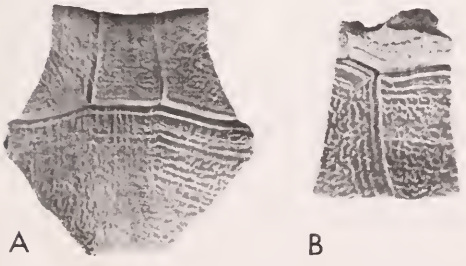

Fig. 14. A distinctly sculptured nuchal bone (A) and posterior peripheral bone (B) of *Deirochelys carri* from the Love Bone Bed.

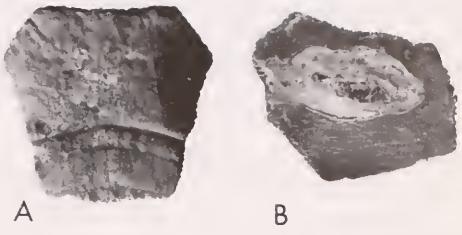

Fig. 15. *Deirochelys* fossils from the Thomas Farm Miocene (x 1.1); (A) neural bone, (B) visceral surface of pleural bone fragment showing rib juncture scar.

DISCUSSION

The material now available shows that the genus *Deirochelys,* instead of being an evolutionary enigma, possesses one of the most complete evolutionary records of any Recent turtle. Evolution of *Deirochelys* has been by specialization of a generalized emydine stock (presumably *Chrysemys*). The earliest fossils are, in fact, difficult to distinguish from *Chrysemys.* We may estimate by extrapolation at what point the two genera would be no longer distinct — i.e., the time at which a generalized turtle began its initial shift to a new adaptive zone in response to selective pressure. The elongated neck (and presumably skull) as well as associated muscular (Shah, 1963) and osteological modifications of *Deirochelys* had already developed by middle Pliocene. This character suite is already conspicuous in hatchling *D. reticularia,* so that phylogenetic recapitulation must occur very early during ontogenetic development if it occurs at all. The divergence from a more generalized aquatic emydine stock (moderately short

neck, long neural bones, weak hyoid apparatus, robust ribs emerging from very near the proximal ends of pleural bones, limited trunk vertebral musculature, and a relatively broad shell, as in the genus *Chrysemys)* had certainly begun by the Miocene. Extrapolations based on an average rate of evolution from such a generalized ancestor suggests an Oligocene origin of the genus (Fig. 16). This character suite almost certainly evolved as a peculiar trophic structure; *Deirochelys* utilizes a "pharyngeal" method of feeding (Bramble, 1973) for capturing prey capable of quick movements (primarily aquatic arthropods). Arguments such as those of G. J. W. Webb and Johnson (1972), in which cervical elongation is held to represent a thermoregulatory device, seem at most of secondary significance in this case, particularly in light of the hypertrophied hyoid skeleton.

The thick shell of *D. carri* and the Thomas Farm *Deirochelys,* as well as of Blancan and Irvingtonian *D. reticularia* (Table 2), suggests that until Late Pleistocene *Deirochelys* was a moderately thick-shelled turtle. Pleistocene reduction in weight and volume of the shell may have allowed faster pursuit and increased maneuverability necessary for capturing fast-moving prey (author's unpublished data) on which *Deirochelys* had come to specialize. Loss of armor (if the thick shell served this purpose) may have been offset by crypsis and behavioral immobility (unpublished observations). In addition to changes in shell thickness, general reduction in body size, accompanied by relative elongation and heightening of the shell, seems to have occurred from at least Hemphillian to Rancholabrean times.

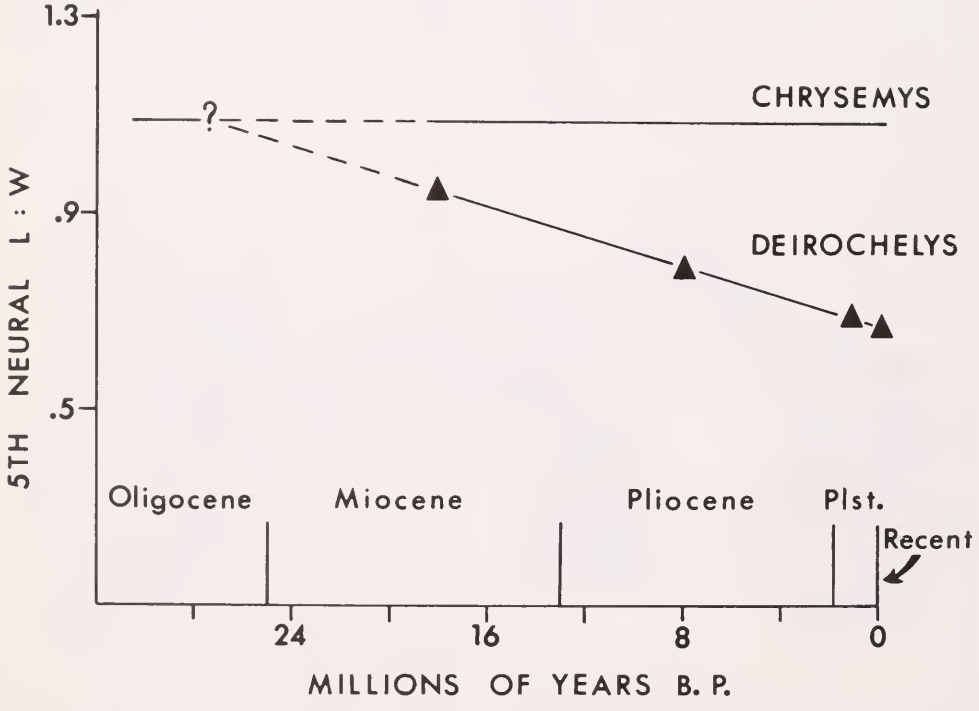

Fig. 16. Extrapolation through time of fifth neural bone length: width ratio of *Deirochelys,* indicating hypothetical point of divergence from a more generalized emydine line.

Relationships. Baur (1889) was the first to hypothesize a close relationship between *Emydoidea* and *Deirochelys* on the basis of similar skull and rib specialization. Although Carr (1952) believed the similarity between *Emys [= Emydoidea] blandingii* and *D. reticularia* to be "purely fortuitous," most subsequent workers supported Baur's idea. Bramble (1974) summarizes the situation:

> Williams (in Loveridge and Williams, 1957) presented a forceful case for a relationship between *Emydoidea* and *Deirochelys*. Although *Deirochelys* possesses no plastral hinge and on many points of shell morphology closely approaches certain members of the genus *Chrysemys* (McDowell, 1964), it does, as Williams noted, share with *Emydoidea* a number of specializations of the skull, cervical vertebrae and neck musculature. On these grounds Williams suggested that *Emydoidea* was a derivative of *Deirochelys* and only convergent with *Emys*. This view has been widely adopted by later workers (Tinkle, 1962; McDowell, 1964; Zug, 1966; Pritchard, 1967; Milstead, 1969; Ernst and Barbour, 1972), some of whom (Tinkle, 1962; Zug, 1966) have presented additional evidence in support of it. McDowell (1964: 275) found no 'significant cranial differences between *Deirochelys* and *Emydoidea*' and accordingly placed both genera in a *Deirochelys* Complex within the Emydinae.

However, Bramble's (1974) study of shell kinesis and other osteological and myological characters indicates instead that *Emydoidea* is a "close phyletic associate of *Emys* and *Terrapene*" as well as of *Clemmys* (the four genera comprising the *Clemmys* Complex), and that these genera may be distinguished as a group from *Deirochelys* and McDowell's (1964) *Chrysemys* Complex. Waagen (1972) formed an identical opinion from his analysis of musk glands in Recent turtles. On the basis of fossils discussed in this paper I agree with the conclusions of Waagen (1972) and Bramble (1974) that *Deirochelys* shares a close relationship with the genus *Chrysemys,* and that similarities between *Emydoidea* and *Deirochelys* are "undoubtedly the result of convergent feeding system" (Bramble, 1974). In fact, most of the modifications used to substantiate a close relationship between *Deirochelys* and *Emydoidea* (elongated ventrally-bowed free ribs, widened neural bones, elongated cervical vertebrae, and a greatly hypertrophied cervical musculature) are also present in the totally unrelated (at least at the familial level) cryptodire genus *Chelydra* as well as the pleurodire genus *Chelus*. They are, moreover, all modifications associated with the pharyngeal method of feeding (Bramble, 1973) employed by these turtles. Hence, the taxonomic use of this particular character suite, so clearly convergent among members of three distinct families, should be treated cautiously in attempts to determine intrafamilial relationships. This paper has presented evidence of the gradual development of these adaptations as a unit of functional morphology (Wilson, 1975) within one of these phyletic lines.

Pleistocene and late Pliocene fossils of *Emydoidea,* which are clearly referable to the extant species *E. blandingii* (Taylor, 1943; Preston and McCoy, 1971), show no special resemblances to late Tertiary *Deirochelys,* other than the convergent character set already discussed, and hence do not support a theory of their divergent evolution. The fossil records and present distributions (Carr, 1952; Preston and McCoy, 1971; Zug and Schwartz, 1971; McCoy, 1973; C. Jackson and Kaye, 1974) indicate that the two genera have remained essentially allopatric, although the southern extension of the range of *Emydoidea* in the late Pleistocene (C. Jackson and Kaye, 1974) just touches the present limit of *Deirochelys* in northeastern Mississippi (C. Jackson and Fortman, 1976). Further ecological studies might help to determine if this allopatric relationship reflects a Gause-type competitive relationship or a difference in thermal requirements.

Distribution and Paleoecology. The genus *Deirochelys* is endemic to the southeastern United States, and it is therefore not surprising that the first extensive evidence of its fossil history should be from Florida. All vertebrate fossil sites known to contain *Deirochelys* (Fig. 1) occur within the range of the modern subspecies *D. reticularia chrysea* or its zone of intergradation with *D. r. reticularia* (Schwartz, 1956; Zug and Schwartz, 1971).

Deirochelys reticularia usually inhabits quiet, shallow bodies of freshwater throughout its range although it occasionally enters the quieter portions of streams (Pope, 1939; R. Webb, 1950; Carr, 1952; Schwartz, 1956; Campbell, 1969) and perhaps rarely saltwater (Neill, 1948; Martof, 1963). Personal observations in north-central Florida indicate that the densest populations of *Deirochelys* occur in shallow (less than one meter) ponds with abundant basking logs, emergent bushes (e.g., *Cephalanthus)* and an extensive *Lemna-Wolffiella* surface mat. From a structural standpoint, the relatively short limbs, long nuchal scute underlap, and absence of streamlining (as compared to a lotic from such as *Chrysemys concinna)* reflect its evolution as a quiet-water form. The turtle also shows a proclivity for overland wandering (Neill, 1948; Carr, 1952; Gibbons, 1969, 1970). Its typical association with the southeastern Coastal Plain (Mount and Folkerts, 1968) implies adaptation to a warm temperate climate. The presence of *Deirochelys* and associated fauna *(Lepisosteus, Amia, Alligator, Chrysemys caelata* [D. Jackson, 1976], *Trionyx* cf. *T. ferox)* in Hemphillian sites thus indicates the existence of quiet freshwater (e.g., sinkhole ponds or sluggish streams) and a warm, equable climate in the Florida middle Pliocene.

Even in the most favorable habitats *Deirochelys* today rarely reaches densities comparable to those of sympatric emydine turtles (e.g., *Chrysemys nelsoni, C. floridana, C. scripta).* This relationship appears to hold also in the Pliocene; in the only Pliocene deposit containing large numbers of *Deirochelys* (Love Bone Bed), *Chrysemys caelata* elements outnumber those of *D. carri* approximately four to one. In what presumably was a suboptimal habitat for *Deirochelys* at McGehee Farm the ratio is even more disparate. This indicates that populations of *Deirochelys* may be more restricted by limiting factors than are other emydines.

All fossil records for *Deirochelys* from sites near the present coastline of Florida (Fig. 1) are either sub-Recent or late Rancholabrean. All other sites except those in the Waccassassa River are in presently well-drained localities 21 to 37 m above present sea level; these include all sites assigned to the Hemphillian, Irvingtonian, Blancan, and early Rancholabrean periods.

S. D. Webb and Tessman (1968) have presented vertebrate faunal evidence supporting conclusions based on physiographic evidence (Alt and Brooks, 1964; Alt, 1967) that sea level dropped and rose again as much as 30 meters during Hemphillian (middle Pliocene) time. McGehee Farm (early Hemphillian) was thus very near the Pliocene coastal shoreline during its time of deposition and its fauna clearly reflects an estuarine influence, although nearby Mixson's Bone Bed, which occurs at the same elevation, does not (S. Webb and Tessman, 1968). Additionally, the late Pliocene and middle Pleistocene interglacial deposits containing *Deirochelys* were much nearer to coastal shorelines during deposition than they are today. It seems probable that since at least the Pliocene, *Deirochelys* has been associated primarily with lowland habitat, as was the Pleistocene box turtle subspecies *Terrapene carolina putnami* in Florida (Auffenberg, 1958). Distribution of these turtles in the Florida peninsula and along the Gulf of Mexico coast must have fluctuated with the advance and retreat of the Pleistocene sea. The proclivity of the genus for overland wandering has probably been instrumental in maintaining or reestablishing inland populations at higher elevations in the abundant perched lakes (bodies of water which are completely above the piezometric surface and sometimes subject to spontaneous drainage) common throughout much of the peninsula today. The present inland populations may be relicts of higher sea levels or terrestrially-reestablished populations.

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Appendix
Fossil Localities Containing *Deirochelys*

Miocene: Hemingfordian site

Thomas Farm, Gilchrist County.

Auffenberg (1963a) reviews the geology and literature pertinent to this site in addition to discussing its ophidian fauna. He interprets the site as representing a lower Miocene fissure fill and points out biotic evidence for the presence of slow-moving or still water during that time. Formerly considered Arikareean by most workers, the fauna has recently been reinterpreted as medial Hemingfordian (Patton, 1969; Tedford and Frailey, 1976). Thomas Farm is the type locality of *Geochelone tedwhitei* (Williams, 1953).

Pliocene: Hemphillian sites

Haile VI, Alachua County.

One of a series of Pliocene sites assigned to the "Alachua Formation" of Florida, parts of its paleoherpetofauna have been treated by Auffenberg (1955, 1963a), Goin and Auffenberg (1955), and D. Jackson (1976). Auffenberg (1963a) discusses the stratigraphy of the deposit and states that it represents an ancient stream bed. The site lies approximately 26 m above present sea level.

Love Bone Bed, Alachua County.

This previously unreported site (29°33'N, 82°31'W; Sec. 9, T11S, R18E) near Archer, Alachua County, Florida is named for Ronald Love who discovered it in 1974; it is now being excavated by the Florida State Museum under the supervision of S. David Webb. Preliminary stratigraphic studies reveal that the deposit represents the "Alachua clays" which were laid down in an ancient stream bed cut into uplifted Eocene Ocala Limestone.

The presence of the horses *Hipparion plicatile* Leidy and *Nannippus ingenuus* (Leidy), an early *Osteoborus* dog, the artiodactyls *Synthetoceras* and an advanced *Cranioceras,* and an early saber-cat of the genus *Barbourofelis* (S. D. Webb, pers. comm.), as well as the turtle *Chrysemys caelata* (D. Jackson, 1976), indicates an

early Hemphillian fauna roughly equivalent to that of McGehee Farm and Mixson's Bone Bed.

McGehee Farm, Alachua County.

An early Hemphillian site in the Alachua Formation (Rose and Weaver, 1966; Hirschfeld and Webb, 1968), McGehee Farm is the type locality of the Pliocene emydine turtle *Chrysemys williamsi* (Rose and Weaver, 1966), the tortoise *Geochelone alleni* (Auffenberg, 1966), and the chelydrid *Macroclemys auffenbergi* (Dobie, 1968), and has additionally yielded abundant material representing *Chrysemys caelata* (D. Jackson, 1976) and *Trionyx* sp.

Mixson's Bone Bed, Levy County.

The first known Pliocene deposit (Dall and Harris, 1892; Leidy and Lucas, 1896) within the type section of the Alachua Formation (Simpson, 1929a) of Florida, Mixson's Bone Bed is the type locality of Hay's (1908) *Chrysemys caelata* (D. Jackson, 1976).

Pliocene: Blancan site

Haile XVA, Alachua County.

This deposit represents a former sinkhole filled with alternating coarse sands and clays. The fauna, assigned to the Aftonian interglacial, is characterized by a rich assortment of aquatic and terrestrial vertebrates, including the turtle *Chrysemys platymarginata* (Weaver and Robertson, 1967) for which the site is the type locality. Although now 24 m above present sea level the presence of marine vertebrates in the fauna indicates higher sea level during deposition and a decided estuarine influence (Kinsey, 1974; S. Webb, 1974). Robertson (1976) presents a detailed account of the stratigraphy and the mammalian fauna of the deposit.

Pleistocene: Irvingtonian site

Haile XVI, Alachua County.

An undescribed pit (29°40'40"N, 82°34' 20"W; Sec. 25, T9S, R17E) in the Haile limestone quarries (Ligon, 1965) excavated by the Florida State Museum under the supervision of S. David Webb in May, 1973. The fauna appears to be interglacial, of Irvingtonian age, and may represent the first known Yarmouthian deposit in Florida. A more detailed discussion of the deposit will accompany reports of faunal studies presently being conducted.

Pleistocene: Rancholabrean sites

Bradenton 51st Street, Manatee County.

A coastal marsh 3 m above present sea level (S. Webb, 1974), the site is discussed by Simpson (1930a, b) and Auffenberg (1958; 1963a) and is now known to represent the Sangamonian interglacial (S. Webb, 1974).

Coleman III C, Sumter County.

An undescribed deposit (Sec. 7, T20S, R23E) of Rancholabrean age (S. D. Webb, pers. comm.), this site, like previously reported Coleman deposits (Martin, 1974), represents a filled sinkhole in the late Eocene Ocala Limestone; its surface lies approximately 24 m above present sea level.

Kendrick IA, Marion County.

A sinkhole-fissure fill near Kendrick, the deposit lies approximately 24 m above present sea level. Kurten (1965) and Brodkorb (1959) assign the fauna to the Illinoian or early Sangamonian although Auffenberg (1958) and S. Webb (1974) believe it to represent the Wisconsinan.

Reddick IIC, Marion County.

Approximately 24 m above present sea level, this inland deposit represents a Pleistocene sinkhole or fissure fill containing a Rancholabrean fauna (S. D. Webb, 1974).

St. Petersburg, Catalina Gardens, Pinellas County.

A small, previously unreported deposit (Sec. 12, T32S, R16E) at approximately present sea level, its fauna is apparently Rancholabrean in age (S. D. Webb, pers. comm.).

Seminole Field, Pinellas County.

A Pleistocene coastal marsh 3 m above present sea level, Simpson (1929a), Auffenberg (1958) and Kurten (1965) assign this site to the Wisconsinan glacial period. Cooke (1926) and Simpson (1929a) give accounts of the stratigraphy of the deposit. Simpson (1929a, b, 1930b) lists the mammalian fauna, and Gilmore (1938), Brattstrom (1953) and Auffenberg (1963a) the snake fauna.

Vero, Indian River County.

Only 3 m above present sea level, this site is considered by most recent authors (Weigel, 1962; Auffenberg, 1963a; Webb, 1974) to represent the late Wisconsinan glacial period. Weigel (1962) discusses its stratigraphy and vertebrate fauna (but does not include *Deirochelys*) and reviews the extensive literature pertaining to the site.

Waccasassa River I, V, and VI, Levy County.

Although S. Webb (1974) includes site VI in his chronology of Florida Pleistocene localities, neither of the other deposits which have yielded *Deirochelys* (I, Sec. 20 and V, Sec. 32, T13S, R16E) has been mentioned. The sites are 6 - 7 m above present sea level and contain Rancholabrean faunas (S. D. Webb, pers. comm.).

Wall Company Pit, Alachua County.

The stratigraphy of this small fissure deposit is briefly discussed by Auffenberg (1963a). Auffenberg (1958) tentatively assigns the deposit to a time between the Illinoian glacial maximum and the Sangamonian interglacial maximum.

Sub-Recent sites

Nichol's Hammock, Dade County.

Hirschfeld (1968) describes the geology, paleoecology, and vertebrate fauna of this solution hole site. Her herpteofaunal list includes *Deirochelys reticularia.*

Warm Mineral Springs, Sarasota County.

Ferguson et al. (1947) describe the hydrology and topography of this spring (Sec. 25, T39S, R20E, less than 6 m above present sea level) under the name of Warm Salt Spring. Clausen et al. (1975) present a detailed description of the geology of the deposit for which they report a radiocarbon age of approximately 10,000 years. Fossils are currently being excavated by the Florida Department of State under the direction of W. A. Cockrell.

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SYSTEMATICS OF THE CRAWFISHES OF THE HAGENIANUS GROUP OF THE GENUS *PROCAMBARUS*, SUBGENUS *GIRARDIELLA* (DECAPODA, CAMBARIDAE)
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TULANE STUDIES IN ZOOLOGY AND BOTANY

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SYSTEMATICS OF THE CRAWFISHES OF THE HAGENIANUS GROUP OF THE GENUS *PROCAMBARUS*, SUBGENUS *GIRARDIELLA* (DECAPODA, CAMBARIDAE)

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ABSTRACT

The Hagenianus Group of the crawfish genus *Procambarus* represents those members of the subgenus *Girardiella* which occur east of the Mississippi River and south of the Ohio River. Standard taxonomic procedures and morphometric analyses revealed that there are five distinct species, four of which are new [named *P. (G.) barbiger, P. (G.) cometes, P. (G.) connos,* and *P. (G.) pogum*], and that *P. hagenianus* exists as two subspecies, one previously undescribed and herein named *vesticeps.* The most conspicuous feature of the undescribed taxa is a beard of setae along the mesial margin of the palm, especially in Form I males. Significant morphological distinctions exist in the first pleopods of males, in the annuli ventrales of females, in the chelipeds and in the antennal scales. The group is nearly unique in possessing stout spines which extend beyond the distal margin of the mesial ramus of the uropods; it is unique in the subgenus in that all members lack a cephalic process on the first pleopod. Data suggest close relationships with *P. (G.) tulanei* Penn and a single invasion of their present habitats from the north via the upper coastal plain. There is no evidence of clinal variation, and the species are neither more nor less variable, inter- or intraspecifically, than other crawfishes similarly studied.

The first record of the existence of the crawfishes currently assigned to the subgenus *Girardiella* was the publication of a figure and a description of a single specimen of a Form I male from "Charleston, South Carolina [U.S.A.]" mistakenly identified as *Cambarus carolinus* of Erichson (1846) in Hagen's monograph (1870). The next extensive treatment of the North American crawfishes was by Faxon (1884); it noted the misidentification of the specimen and asserted that it represented an undescribed species. Faxon proposed the name *Cambarus hagenianus* for the species (p. 141), and the single Form I male became the type by monotypy. Following receipt of additional specimens from State College (Oktibbeha Co.) and Muldon (Monroe Co.), Mississippi, and Farmdale (prob. Faunsdale, Marengo Co.), Alabama, he published additional descriptive information, observations on variation and color illustrations of Muldon specimens (Faxon, 1914:366-367, Pl. 1). Among the morphological variations mentioned, the most prominent feature, perhaps, was the bearding of the hand seen in Muldon males. No further taxonomic data on the Hagenianus Group were published until Lyle (1938) presented an abstract of the dissertation he submitted to Iowa State University. In the abstract he alluded to the existence of four distinct breeding populations by the publication of subspecific *nomina nuda;* at the same time he proposed the subgenus *Girardiella* to receive these and the nominate subspecies of *C. hagenianus* Faxon. The species was assigned without comment to the genus *Procambarus* by Hobbs (1942a) when he elevated most of Ortmann's (1905a, 1905b, 1906) subgenera of *Cambarus* to generic rank. Later, in a revision of the genus

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Procambarus, he accepted *Girardiella,* refined its definition and assigned additional taxa to the subgenus (Hobbs, 1972a). Nomenclatorial and taxonomic data on the described taxa were amply presented in the paper. Fitzpatrick (1968) gave a preliminary report of the status of the several taxa mentioned by Lyle *(op. cit.),* and in a later paper he summarized the results here presented in proper taxonomic detail, along with observations on the general biology and economic impact of the several taxa (1975). In the same paper he proposed that the subgenus be divided into two groups, Hagenianus and Gracilis. The species herein treated represent the entirety of the former group.

The common name usually applied to the members of the Hagenianus Group is "prairie crawfishes." This alludes to their distribution being principally in the prairie soils of eastern and central Mississippi and western Alabama. Although the type-locality is given as "Charleston, South Carolina," this surely is in error. Collections along the eastern seaboard have not revealed *P. hagenianus,* or even a near relative. The primary burrowing crawfishes *(sensu* Hobbs, 1942b) of the Charleston area are members of either *Cambarus* or *Fallicambarus* (Hobbs, 1972b).

In 1964 the collections on which Lyle had based his designations of the *nomina nuda* were located at Mississippi State University and transferred to the National Museum of Natural History. These specimens validated Lyle's contentions that there are several breeding populations of the taxon heretofore referred to as *Procambarus hagenianus* (Faxon). Fitzpatrick (1968) examined the Mississippi State University material and additional collections and discerned that each of Lyle's "subspecies" was a distinct taxon, and that two more taxa were represented. Following these morphological studies, the several populations were subjected to morphometric analysis and the parameters and limits of variation determined. This paper is a presentation of the results of those efforts.

During the course of these studies, the late Dr. Lyle was generous with his time and knowledge in helping me reconstitute the data on the collection and supplied many first-hand reminiscences of circumstances under which collecting was effected. Dr. Horton H. Hobbs, Jr., generously assisted via conversations, discussions, collecting and providing color photographs and field records. Drs. Horton H. Hobbs III, James F. Payne and Shih-ming Chien assisted in the field work, as did Messrs. Warren G. Anding and J. Paul Thaxton. The facilities of the National Museum of Natural History were made available on several visits. Randolph-Macon Woman's College, Lynchburg, Virginia, provided the time necessary for the mathematical computations on its Honeywell 1642 time-share digital computer. Ms. Barbara A. Laning provided clerical/technical assistance during much of the course of the study. The Research Committee of the University of South Alabama provided funds for preparation of the manuscript.

Specimens examined are designated as follows: Museum of Comparative Zoology (MCZ), National Museum of Natural History (USNM). Specimens not designated by a specific museum are in the collection of the writer, deposited at, but not yet catalogued by, the National Museum of Natural History, Smithsonian Institution.

The Hagenianus Group

Those members of the subgenus *Girardiella* Lyle of the genus *Procambarus* Ortmann which occur east of the Mississippi River flood plain were assigned to a newly created Hagenianus Group by Fitzpatrick (1975:384). He based his subdivision of the subgenus on morphological, geographic and evolutionary data. Because *P. hagenianus* is, by monotypy, the type of the subgenus *Girardiella,* the precise identity of this species is important. Hagen (1870) originally published figures and a description of a series which he called *Cambarus advena,* but Faxon (1884:140-141) tells us that the figures and descriptions were transposed with those of *C. carolinus,* according to Hagen's labels. Faxon then proceeded to rename Hagen's *carolinus* (described and figured as *advena) C. hagenianus.* For the identity of the several specimens called *advena*

by Hagen, see Hobbs (1974:47). Fortunately, however, the original description was based on a single specimen, which therefore becomes the type of the species and allows for precise definition. The matter is further complicated by the designated type-locality, Charleston, S.C. Animals compatible with the type do not occur within several hundred miles of Charleston. Hagen (1870:88) simply lists "Cat. 232, Charleston, S.C., Professor L. Gibbes. Male. Fem. / Spec. 2.", but Faxon (1914:366) adds that ". . . the type specimen . . . [was] received early in the history of the Museum [of Comparative Zoology, Harvard University] from Professor Lewis R. Gibbes of Charleston, S. C." Curatorial practices, even at leading museums, were not as stringent as they are today, and it was common for specimens received from a "cabinet," especially a famous one such as that of Professor Gibbes, to carry with them a locality designating the location of the cabinet rather than of the collection. Such seems to be the case with the type in question. The specimen probably was collected somewhere in the Black Belt of Alabama or Mississippi (see *"Range"* comments below).

Morphologically, the Hagenianus Group is distinct from the Gracilis Group which occurs west of the Mississippi River flood plain. In the Gracilis Group only *P. tulanei* Penn (1953) possesses a beard of plumose setae along the mesial margin of the palm of the cheliped in the Form I male; in the Hagenianus Group only *P. hagenianus (sens. str.)* lacks it. Another striking difference exists in the spinose ornamentation of the uropods. In the Hagenianus Group, all individuals bear two stout, acute spines on the mesial ramus of the uropod which project well beyond the distal margin of the ramus – one from the lateral corner and one from the median ridge. In *Procambarus* this characteristic is shared only with *P. (Acucauda) fitzpatricki* Hobbs (1971). The only other cambarid crawfish known to bear these spines with such a degree of development is *Fallicambarus (F.) macneesei* (Black, 1967) (Hobbs, 1973). Far more significant, however, are the differences in the first pleopods of Form I males. In all of the taxa of the Hagenianus Group a cephalic process is lacking, while this structure is present, albeit in varying degrees of development, in all members of the Gracilis Group. These differences are reflected in the structure of the pleopods of Form II males, but, in keeping with the usual lesser development of their secondary sexual characteristics, are less obvious.

MATERIALS AND METHODS

Each specimen was subjected to 10 measurements: (1) carapace length, (2) rostrum length, (3) rostrum width, (4) antennal scale length, (5) antennal scale width, (6) areola length, (7) chela length, (8) length of inner (= mesial) margin of palm, (9) palm width, and (10) dactyl length; in addition, in males pleopod length was measured. Techniques of measurement were those employed by Fitzpatrick (1967). For analyses of intra- and interspecific variability, appropriate ratios were calculated (except for carapace length), arcsine transformations performed, and the appropriate statistical procedures followed; additionally, the ratios were subjected to statistical analysis without transformation, and the results are presented graphically using Fitzpatrick's *(op. cit.)* method (Figs. 109-119).

Meristic and qualitative data were collected on the nature and quantity of setation on the inner margin of the palm and mesial margin of the dactyl, as well as the tubercular ornamentation of these structures. Similar data were collected for setation of the proximal podomeres of the third maxilliped. Data were accumulated concerning numbers and distribution of tubercular ornamentation on the opposable margins of the dactyl and immovable finger, and the standard morphological observations were made. Color notes and photographs were made on field collections by the writer, Hobbs, Jr., and Hobbs III; data made available by the latter two are incorporated where appropriate. Where notes were otherwise lacking, reference is made to Lyle's dissertation (1937) for color patterns.

In subsequent discussions, unless otherwise noted, all lengths are expressed as the ratio of carapace length to the specific measurement; consistently different are length of mesial margin of palm and dactyl length, both of which are expressed as ratios to chela length. Widths are expressed as ratios to the length of the particular structure.

Procambarus (Girardiella) hagenianus hagenianus (Faxon, 1884:141)
Figures 1-18

Cambarus advena. — Hagen, 1870:86, 87, figs. 90-92, (?)164; Fowler, 1912:567.

Cambarus Carolinus. — Hagen, 1870:31, 32, 53, 74, 75, 88 (part); Faxon, 1885:8, 9, 48, 54 (part), 55, 56, 58 (part), 65 (part), 158 (part), 167 (part), 173 (part).

Cambarus carolinus. — Brocchi, 1875:27; Faxon, 1884:140-141 (part); Ortmann, 1902:277, 279; Faxon, 1914:366; Hobbs and Villalobos, 1964:321, 322.

Cambarus Hagenianus. — Faxon, 1884:141; 1885:56.

Cambarus hagenianus. — Hay, 1902:38; Harris, 1903:58, 101, 137, 138, 154; Ortmann, 1905a:104; 1905b:438; Faxon, 1914:366-367, 412, Pl. I, Pl. VII: figs. 1, 7; Carr, 1936:1-11 (part); Lyle, 1938: 75; Hobbs, 1938:65; 1972a:7; Martin and Uhler, 1938:140; Hobbs and Villalobos, 1964:322; Fitzpatrick, 1975:381.

Cambarus (Cambarus) hagenianus. — Ortmann, 1905a:101.

Cambarus (Ortmannicus) hagenianus. — Fowler, 1912:341 (by implication). crawfish or crayfish. — Fisher, 1912:321-324, fig. 1 (probably *C. hagenianus* x *vesticeps).*

Cambarus (Girardiella) hagenianus hagenianus. — Lyle, 1938:76 (by implication).

Procambarus hagenianus. — Hobbs, 1942a:342 (by implication); 1942b:35, 71, 109; 1959:887; 1968:K9 (part); 1971:461, 466, 467; 1972a:4; Penn, 1953:166; Pennak, 1953:455; Smith, 1953:94; Fitzpatrick, 1968:37 (part); Dowell and Winier, 1970:489; Smiley and Miller, 1971:221; Momot and Gall, 1971:363; Payne, 1972:27; Hobbs and Bouchard, 1973:52; Reimer, 1975:25.

Procambarus (Girardiella) hagenianus. — Hobbs, 1972a:7, figs. 2d, 7a-g; 1972b:47 (part), 151 (part), 161 (part) (by implication), 162 (part) (by implication), figs. 21a, 39d, 40b; 1973:461; 1974:47 (part), fig. 192; Hobbs and Bouchard, 1973:63; Fitzpatrick, 1975:381, 382, 383, 384, 385, 387, 388.

Diagnosis. — Body pigmented, eyes small but well-developed. Rostrum (Fig. 5) with gently converging, rarely subparallel margins, lacking marginal spines; acumen short, indistinctly delimited basally. Areola 37.22-44.14% (avg. 42.00) of entire length of carapace; areola linear. Carapace devoid of cervical spines or tubercles. Suborbital angle absent, rarely obsolete (Fig. 11). Postorbital ridges lacking spines or tubercles cephalically. Cephalic portion of epistome (Fig. 18) subtrapezoidal in outline, usually with small cephalomedian tubercular projection. Antennal scale (Fig. 15) 1.59-3.31 (avg. 2.38) times longer than wide, widest distal to midlength, thickened lateral portion terminating distally in strong acute spine, which spine approximates 21% of entire length of scale. Mesial margin of palm (Fig. 14) devoid of conspicuous setiferous beard, instead with mesial row of 6-7 tubercles, and second row of 4-5 tubercles medial to it; upper and lower surface of palm covered with setiferous punctations; palm of female (Fig. 13) similar. Opposable margin of immovable finger with row of three small, one large and one small spine in proximal one-half, and crowded minute denticles in distal half, single ventromedially directed tubercle at base of distal one-fourth; opposable margin of movable finger slightly excavated in basal third, with two tubercles in excavation, middle one-third with row of one large, two small and one slightly removed small tubercle, crowded minute denticles in distal third and between penultimate and ultimate tubercle of margin. Ischia of third pereiopods only bearing hooks (Fig. 12); no prominences or bosses on coxae of third through fifth pereiopods. Mesial ramus of uropod (Fig. 16) with two conspicuous spines, median larger, projecting beyond distal margin. First pleopods (Figs. 1, 3, 4, 6, 7, 9, 10) symmetrical, shoulder present at base of central projection, pleopods reaching approximately to midlength of coxae of third pereiopods when abdomen flexed; distal extremity bearing (1) prominent acute mesial process directed caudodistally, extending beyond other terminal elements approximately by length of central projec-

tion, mesial process curving gently laterally in distal half; (2) well-developed central projection with apical portion bent laterally, centrocephalic process, centrocaudal process and mesial surface of mesial process enveloped at base by closely applied fold continuous with caudal surface of mesial process; and (3) conspicuous subrectangular (in lateral aspect) caudal process extending distally subparallel to central projection, caudodistal portion lamelliform; pleopods of second form male (Figs. 2, 8) less well developed and non-corneous. Annulus ventralis of female (Fig. 17) deeply excavate cephalomesially, with sulcus sloping precipitously toward cephalic margin, flanked laterally and/or cephalically by prominent ridges elevated (ventrally) two to three times height of remainder of annulus above sulcus, usually one cephalic and one lateral, each terminating in two or three tubercles; sinus originating in deep transverse fissure in cephalolateral quarter, running subparallel to longitudinal axis of animal to about middle of annulus, arcing sharply cephalomedially to approximately center then joining accessory sinus running from center of annulus to caudal one-fourth; postannular sternite subconical in shape.

Type. – MCZ no. 232. Male, Form I; by monotypy.

Type-locality. – Charleston, South Carolina. Clearly in error; see discussion above.

Range. – *P. hagenianus (sens. str.)* has been collected in association with the prairie soils, south and east of Tibbie Creek in the Tombigbee drainage of Lowndes, Noxubee and Oktibbeha counties, Mississippi, and Marengo, Pickens and Sumter counties, Alabama (Fig. 120). The easternmost and southernmost record is that given by Faxon (1914:366) as "Farmdale, Ala." (USNM no. 41462 and a derivative series, MCZ no. 7371). No record of such a town can be found, but a Faunsdale (Marengo County) does exist in the Black Belt. Considering that many labels were kept in script at that time, the emended spelling probably is correct. Specimens from the vicinity of Jackson, Mississippi (USNM no. 93101), probably represent mislabeled collections; this is discussed at greater length in the consideration of the range of *P. barbiger,* below. *The species does not exist in South Carolina.* The relationships of this race with a subspecies described below are discussed with the latter.

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Color. – As with all members of the Hagenianus Group, *P. hagenianus* is intensely colored and can be found in two color phases—one basically blue, the other basically red. Both phases, except for the base colors, are marked essentially the same. The blue phase is usually deep, nearly royal, blue, the intensity of which is accentuated by creamy-white rostral margins, postorbital ridges and often the finger tips. Lateral areas of the carapace are provided with a purplish blush which often extends onto a tan or reddish-brown abdomen. Hobbs, Jr., (personal communication) has provided me with his color notes of a red phase Form I male collected in Sumter County, Alabama. This is the most thorough description of a crawfish color I have seen, and he has generously given me permission to quote it as follows—

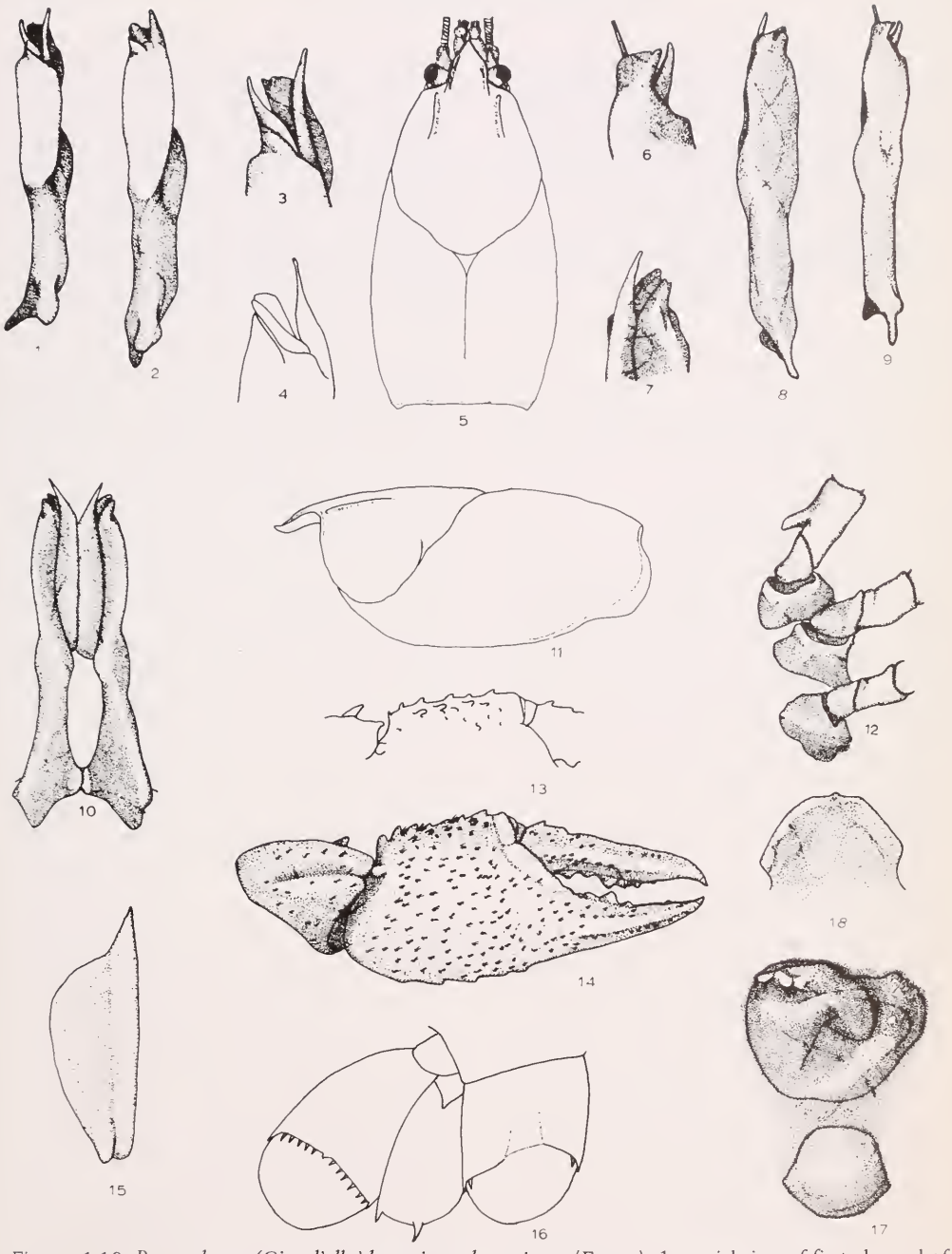
> "Cephalic section of carapace with rostral and postorbital ridges canary yellow to orange cream. Dorsum between ridges dark orange-tan. Dorsal part of hepatic region and area over mandibular muscle brick red; narrow reddish brown yoke, contiguous with cervical groove, joining caudal portions of red area across median line. Cream-tan arc extending from antennal region along and dorsal to cervical groove reaching level of cervical

tubercles. Tubercles in hepatic region tipped with cream to yellow. Cephalic triangular rudiment of areola reddish brown; branchiostegites olive with tan suffusion dorsolaterally and almost white laterally, part flanking cervical groove margined in orange cream dorsally and brick red laterally. First abdominal segment orange with pale markings on reduced pleura; cephalic segment of tergum of second segment with narrow dark red band; remainder of abdomen reddish brown dorsally with pleura brownish basally and almost cream marginally. Cephalic section of telson with paired brownish spots, remainder of tailfan orange tan flecked with brown. Eyestalks orange brown; peduncles of antennules and antennae mostly orange but with brown mottlings; flagella and antennal scale orange, tip of spine of latter pale pinkish cream. Cheliped basically orange with tan suffusion; spines on all podomeres and mesial row of tubercles on palm tipped with orange cream; tubercles on dorsal surface of palm and proximomesial surface of dactyl reddish brown. Remaining pereiopods and third maxillipeds orange with olive suffusion. Sternal areas pale orange to cream."

Variation. — Most of the variations encountered in this species are covered in the *"Diagnosis"* above or in the preceding discussion of color pattern. The usual variation of development of spinose and tubercular ornamentation is encountered, but I believe that the majority of such is the result of injury and/or wear and is not an inherent feature of the species. One often finds males, especially of Form I, in which the distal margin of the caudal process is sinuate or serrate, but this is due to in-life or *postmortem* breakage, as many specimens have a perfect margin on one pleopod and a sinuous or serrate margin on the other. This observation is valid for all members of the Hagenianus Group. Additionally, one should consider the variations noted for the subspecies following, especially the features seen in what I believe to be intergrades.

The results of morphometric analysis are as follows (based on 110 specimens: 54 ♂♂I, 9 ♂♂II, 47 ♀♀). Carapace length for Form I males was 23.9-39.0 (avg. 33.11), for females 27.8-40.4 (avg. 33.95) and for males, Form II, 25.5-32.7 (avg. 30.00). Form I males had a rostral length of 4.51-6.19 (avg. 5.14), females 4.16-5.82 (avg. 5.09) and Form II males 4.40-6.71 (avg. 5.22). The rostrum was 1.08-1.63 (avg. 1.40) times longer than wide in Form I males, 1.12-1.61 (avg. 1.36) times in females and 0.70-1.59 (avg. 1.36) in Form II males. Areola length was 2.27-2.69 (avg. 2.38) in Form I males, 2.30-2.53 (avg. 2.43) in females and 2.32-2.56 (avg. 2.44) in males, Form II. In Form I males antennal scale length was 6.53-9.52 (avg. 7.96), in females 6.08-9.13 (avg. 8.06) and 6.96-11.48 (avg. 8.67) in Form II males. Chela length in Form I males was 1.31-1.55 (avg. 1.41), in females 1.44-1.83 (avg. 1.61) and in Form II males 1.38-1.69 (avg. 1.53). Chela width was 2.03-2.53 (avg. 2.29) in Form I males, 2.01-2.43 (avg. 2.21) in females and 2.09-2.59 (avg. 2.36) in Form II males. Length of the inner margin of the palm was in Form I males 2.40-3.23 (avg. 2.82), 2.42-2.94 (avg. 2.67) in females and 2.56-2.97 (avg. 2.82) in Form II males. In males, Form I, dactyl length was 1.53-2.27 (avg. 1.67), in females 1.51-1.92 (avg. 1.72) and in Form II males 1.70-1.84 (avg. 1.76). Pleopod length was 2.88-4.05 (avg. 3.28) in Form I males and 3.21-5.43 (avg. 3.60) in Form II males. Table 2 gives the carapace length limits for all taxa.

Specimens examined. — ALABAMA: Marengo Co., Faunsdale (= "Farmdale"), 27 June 1910 (3 ♂♂I, 6 ♀♀), (1 ♂I, 1 ♂II, 1 ♀); Sumter Co., 2.8 mi. N of U.S. Hy. 11 on St. Rte. 39, along Jones Creek, 12 April 1974 (1 ♂I, 1 ♀ imm.); MISSISSIPPI: Hinds or Rankin Co., "near Jackson" (?), 6 May 1936 (2 ♂♂I, 1 ♂II, 16 ♀♀), (3 ♂♂I, 2 ♀♀); Lowndes Co., Mahew, 1 April 1936 (1 ♂I, 1 ♂II, 11 ♀♀), 4.5 mi W Columbus, 2 May 1936 (8 ♂♂I, 2 ♂♂II, 5 ♀♀); Noxubee Co., 6 mi E. of Macon, 6 March 1936 (11 ♂♂I, 5 ♂♂II, 6 ♀♀,1 ♀); Oktibbeha Co., Agricultural College (= Mississippi State University, = MSU), 11 and 13 March 1911 (1 ♂I, 9 ♀♀), 4 April 1911 (1 ♀), (1 ♂II, 11 ♀♀, 1 ♂imm., 1 ♀imm.), 11 May 1911 (2 ♀♀), 23 February 1912 (6 ♀♀), (6 ♀♀), 27 March 1916 (1 ♀), 1935 (17 ♀♀), Spring, 1936 (5 ♂♂I, 1 ♀), 26 April 1967 (1 ♂I, 2 ♀♀), 8 May 1967 (1 ♀), 7 April 1969 (1 ♀), (1 ♀), (1 ♀), (2



Figures 1-18. *Procambarus (Girardiella) hagenianus hagenianus* (Faxon): 1, mesial view of first pleopod of Form I male; 2, mesial view of first pleopod of Form II male; 3, terminal elements of first pleopod of Form I male, mesial view; 4, terminal elements of first pleopod of Form I male, cephalic view; 5, dorsal view of carapace of Form I male; 6, terminal elements of first pleopod of Form I male, lateral view; 7, terminal elements of first pleopod of Form I male, caudal view; 8, lateral view of first pleopod of Form II male; 9, lateral view of first pleopod of Form I male; 10 caudal view of first pleopods of Form I male; 11, lateral view of carapace of Form I male; 12, proximal podomeres of third through fifth pereiopods of Form I male; 13, mesial margin of palm of female; 14, distal podomeres of cheliped of Form I male; 15, antennal scale of male, Form I; 16, telson and left uropod of Form I male; 17, annulus ventralis and postannular sternite of female; 18, cephalic portion of epistome of Form I male.

♂♂ imm.), (1 ♀ imm.), (1 ♀), (1 ♀), no date (1 ♀), just SW of Starkville city limits, 7 July 1968 (1 ♂I, 1 ♀), 5 mi. N of Starkville, 1 April 1920 (1 ♂I, 2 ♀♀), Sand Creek, 11 May 1915 (2 ♂♂II, 3 ♀♀), about 10 mi. W of Columbus, April, 1948 (6 ♂♂I, 3 ♂♂II), (25 ♂♂I), "From hole near Chiltons" (Oktibbeha Co. ?), no date (4 ♂♂II, 9 ♀♀).

Procambarus (Girardiella) hagenianus vesticeps n. subsp.
Figures 19 - 36

Cambarus (Girardiella) hagenianus evansi Lyle, 1938:76, *nom. nud.*

Procambarus hagenianus. – Fitzpatrick, 1968:37 (part) (by implication).

Procambarus (Girardiella) hagenianus. – Hobbs, 1972b:47 (part), 151 (part), 154 (part) (by implication).

Procambarus (Girardiella) subsp. A. – Fitzpatrick, 1975:385, 386, 387, 388.

Diagnosis. – Body pigmented, eyes small but well-developed. Rostrum with gently converging margins, lacking marginal spines (Fig. 23); acumen short, indistinctly delimited basally. Areola 34.91-42.78 (avg. 39.85) % of entire length of carapace; areola linear. Carapace devoid of cervical spines or tubercles. Suborbital angle obsolete (Fig. 28). Postorbital ridges lacking spines or tubercles cephalically. Cephalic portion of epistome (Fig. 33) subovoid in outline, lacking cephalomedian tubercle. Antennal scale 2.11-2.94 (avg. 2.46) times longer than wide, widest distal to midlength, thickened lateral portion terminating in strong, but short, acute spine; mesiocephalic margin of lamellar portion with tubercular eminences from which tufts of setae protrude (Fig. 34). Mesial margin of palm (Fig. 32) with dense setiferous beard partially obscuring row of four or five tubercles; mesial margin of movable finger with small spinose tubercle in basal fourth, few setae emerging from distal base of tubercle. Opposable margin of immovable finger with row of two small, two large and one small tubercles in basal half, with crowded minute denticles in distal half, small ventromedially directed tubercle at base of distal fourth. Opposable margin of dactyl slightly excavated in basal third, with two small tubercles in excavation, one large and one small tubercle in remainder of basal half, crowded minute denticles along distal half. Ischia of third pereiopods only with spines; no prominences or bosses on coxae of third through fifth pereiopods (Fig. 31). Inner ramus of uropod with two conspicuous spines projecting beyond distal margin (Fig. 35). First pleopods (Fig. 19, 21, 22, 24, 25, 27, 29) slightly asymmetrical, strong right angular shoulder at base of central projection; pleopods reaching anterior margin of coxae of third pereiopods when abdomen flexed; distal extremity bearing (1) prominent subacute mesial process directed distally and subparallel to main axis of shaft; (2) well-developed central projection with apical portion bent slightly mesially and centrocephalic process enveloped at base mesially, cephalically and laterally by fold continuous with centro-caudal process laterally; and (3) conspicuous, well-developed, subrectangular (in lateral aspect) caudal process extending distally subparallel to central projection for 90% of length of central projection. Annulus ventralis of female deeply excavate cephalically, with strong cephalolateral and/or lateral ridges terminating (ventrally) in three or four tubercles, sinus originating at midlength of annulus in lateral fourth, running transversely to center of annulus then arcing gently to be lost in caudal margin of annulus; postannular sternite broadly conical in shape.

Holotypic male, Form I.—Body subovate, distinctly compressed. Abdomen narrower than thorax (9.3 and 12.6 mm). Width of carapace at caudodorsal margin of cervical groove less than height (12.6, 13.4 mm). Areola 41.58% of total length of carapace and linear; cephalic section of carapace 1.4 times length of areola (Fig. 23). Rostrum depressed (Fig. 28), deeply excavate dorsally, with thickened margins slightly converging cephalically, marginal spines lacking; acumen indistinctly delimited basally; upper surface sparsely punctate, but with usual submarginal row of setiferous punctations. Subrostral ridges moderately well developed to level just below suborbital angle and visible in dorsal aspect to about midlength of rostrum. Branchiostegal spine obsolete. Carapace punctate dorsally and laterally; granulate cephalolaterally with granules best

Table 1. Morphometric differences between Hagenianus Group crawfishes. Upper right half numbers are the numbers of characters in which there is at least 95% probability of difference; lower left half are the numbers in which the probability is 1% or less that there are no differences in the characters tested. Species abbreviations: BA = P. (G.) barbiger; CM = P. (G.) cometes; CN = P. (G.) connus; HH = P. (G.) h. hagenianus; HX = P. (G.) h. hagenianus X vesticeps; HV = P. (G.) h. vesticeps; PG = P. (G.) pogum.

		♂♂ I							♂♂ II						♀♀					
		BA	CM	CN	HH	HX	HV	PG	BA	CM	HH	HX	HV	PG	BA	CM	HH	HX	HV	PG
	BA	X	6	5	8	6	2	4			6	3	1		5	4	5	6	3	3
	CM	4	X	7	7	7	9	5			6	7	7	8	5	6	6	7	6	7
	CN	4	6	X	5	9	8	6			9	5	5	6	7	6	7	5	5	7
♂♂ I	HH	5	7	5	X	7	7	7			10	6	6	6	4	6	6	6	7	5
	HX	8	7	8	7	X	10	8			10	8	8	9	8	9	6	6	8	9
	HV	5	8	7	6	8	X	6			8	5	4	6	8	9	7	9	7	6
	PG	2	5	6	7	7	6	X			5	3	2	2	5	6	6	8	5	6
	BA								X											
	CM									X										
♂♂ II	HH	3	5	7	8	9	8	5			X	8	10	4	9	8	9	10	6	6
	HX	2	6	3	4	7	5	3			8	X	3	3	6	7	8	8	4	5
	HV	1	4	1	5	7	4	1			6	2	X	4	5	5	6	8	4	3
	PG	-	6	1	4	9	5	1			4	2	1	X	4	7	8	9	3	6
	BA	4	5	6	3	6	6	3			8	4	2	4	X	0	9	7	4	5
	CM	4	5	4	5	9	9	5			7	4	4	5	6	X	7	7	9	7
♀♀	HH	5	6	7	6	5	5	5			8	7	6	6	8	7	X	8	7	10
	HX	6	5	5	6	4	9	8			10	6	8	9	6	7	7	X	8	10
	HV	2	5	4	6	8	5	4			5	4	2	2	4	6	7	7	X	11
	PG	2	6	6	5	8	4	3			4	5	2	3	4	5	7	9	9	X

developed just posterior to suborbital angle. Cervical spines or tubercles absent. Cephalic section of telson (Fig. 35) with two spines in each caudolateral corner. Cephalic portion of epistome subovoid in outline, broader than wide, lacking cephalomedian tubercle. Antennules of usual form with well-developed spine on ventral surface of basal segment slightly distal to midlength. Antennae reaching to about caudal margin of carapace; antennal scale 2.4 times longer than wide, widest distal to midlength; thickened lateral portion terminating in strong acute spine approximately 13% of total length of scale.

Ischium of third maxilliped with long, stiff, dense setae arising from mesial margin and long but thinner and sparser tufts arising from ventrolateral margin.

Right chela with palm inflated, moderately depressed; lateral margin tubercular and nearly serrate; entire palmar area covered with setiferous punctations above and below; mesial margin of palm with mat of dense, long setae nearly obscuring mesial row of five strong tubercles, and row of four medial to it, setae arising in tufts from deep punctations; mesial margin of movable finger with two subequal tubercles in basal fourth, each with small tuft of coarse setae arising from cephalic margin, proximal one with tubercular eminence on upper margin. Opposable margin of immovable finger with row of three small, one large and two small tubercles in proximal half, distal half with crowded minute denticles and ventromedially directed tubercle at base of distal fourth; submedial longitudinal ridge above and below, both flanked by setiferous punctations. Opposable margin of movable finger excised in basal third and with two tubercles in excision, additionally one large and two small tubercles in basal two-thirds; distal third provided with crowded minute denticles; with submedian longitudinal ridge only moderately developed above and below, but both flanked with setiferous punctations.

Carpus of right cheliped longer than broad, with strong acute spine at base of distal third of mesial margin, three smaller spinose tubercles in proximal half, single spinose tubercle just distal to aforementioned strong spine; punctate above and below with submedian longitudinal furrow above; distal corners of ventral surface each with strong acute spine, row of two acute spines between ventral mesiodistal spine and strong spine of mesial margin.

Merus of right cheliped with single stout spine on distal dorsal margin and single tubercle just proximal to it; ventromesial margin with row of 13 acute subequal spines plus one strong acute spine distally; ventrolateral margin with row of five subequal acute spines. Ischium with mesial row of three spinose tubercles.

Hooks on ischia of third pereiopods only, directed proximally and extending over about distal third of basis. Coxae of third, fourth and fifth pereiopods lacking eminences or bosses.

First pleopods as described in *"Diagnosis"*; central projection and tip of caudal process corneous.

Uropods (Fig. 35) with mesial ramus bearing two stout subequal spines, one from lateral corner and one from medial ridge.

Sternites and coxae of third through fifth pereiopods bearing long (particularly on sternites) setae partially concealing pleopods when latter held under thorax. Measurements of all types of all taxa are given in Table 3.

Morphotypic male, Form II. – Differing from holotype in following respects: opposable margin of immovable finger bearing four small spines proximal to large spine and two distal to it in proximal half; opposable margin of movable finger with three tubercles (distalmost small) in excision and three tubercles distal to large tubercle; carpus lacking tubercles on mesial margin proximal to and just distal to stout spine. Terminal elements of first pleopod (Figs. 20, 26) less developed than holotype and parts noncorneous.

Allotypic female. – Differing from holotype in following respects: mesial margin of palm (Fig. 30) lacking dense beard, bearing instead three rows of setiferous tubercles, mesialmost row with six stout tubercles,

center row of six squamous tubercles and third row of four squamous tubercles in distal half of inner marginal area, all tubercles with tuft of setae emerging from distal base; upper surface of carpus with oblique row of four tubercles running proximodorsally from stout tubercle of mesial margin with additional two tubercles immediately dorsal to aforementioned stout spine.

Annulus ventralis (Fig 36) deeply excavate cephalomesially with sulcus falling precipitously from middle of annulus to cephalic margin, large cephalolateral and lateral ridges arising approximately twice depth of annulus (ventrally) above sulcus, left more laterally situated and terminating in three tubercles, right more cephalic and terminating in three tubercles, sinus originating in deep fissure at approximately midlength of annulus in right quadrant, running transversely to about center of annulus, then arcing gently sinistrad to be lost in caudal margin; postannular sternite broadly subconical in shape.

Types. – USNM nos. 146265, 146266, 146267 (holo-, allo-, and morphotype, respectively); *Paratypes:* Mississippi: Chickasaw Co. (12 ♂♂I, 2 ♂♂II, 5 ♀♀), Pontotoc Co. (1 ♀). Paratypes located at USNM.

Type-locality. – Egypt, Chickasaw Co., Mississippi.

Range. – This subspecies exists generally north of Tibbie Creek in the Tombigbee drainage of Chickasaw, Clay, Monroe and Pontotoc counties where it is apparently confined to the Black Belt of this area. The northernmost record is from "near Hurracine [*sic,* probably Hurricane; USNM no. 146275], near Thaxton." Southward it intergrades with the nominate subspecies, having an extensive hybrid population in and around Muldon (Monroe Co.). The characteristics of this intergrade population are discussed below under *"Variations."*

Color. – *P. hagenianus vesticeps* differs little in color from *P. h. hagenianus,* except that the colors are paler. I have never seen "red" individuals, but Lyle (1937) reports such. The color plates of Muldon specimens offered by Faxon (1914, Pl. 1) are good representations of the subspecies as I know it; Lyle *(op. cit.)* concurs.

Variations. – Based on morphometric analysis of 29 specimens (16 ♂♂I, 4 ♂♂II, 9 ♀♀). In most morphometric and gross morphological details *P. h. vesticeps* resembles the nominate subspecies. Carapace length for Form I males was 30.3-36.5 mm

TABLE 2. Size parameter ranges in Hagenianus Group crawfishes. All values are of carapace length in mm.

	♂♂I		♂♂II	♀♀
	Max.	Min.	Max.	Max.
P. (G.) h. hagenianus	39.0	23.9	32.7	40.4
P. (G.) h. vesticeps	36.5	30.3	37.9	40.0
P. (G.) h. hagenianus X vesticeps	42.8	27.6	39.0	40.4
P. (G.) barbiger	36.1	24.0		36.6
P. (G.) cometes	37.3	29.6		40.7
P. (G.) connus	41.0	26.6		
P. (G.) pogum	31.1	28.6	34.0	37.4

Table 3. Measurements (in mm) of type specimens of new species and subspecies. All appendages right, except asterisk (*) indicates left.

	Carapace			Rostrum		Areola	Ant. Scale		Cheliped			
	Length	Width	Height	Length	Width	Length	Length	Width	Length	Palm Width	Inn. Mar. Length	Dactyl Length
P. (G.) barbiger												
Holotype	36.1	16.1	19.0	8.0	6.2	15.3			24.1	10.6	8.6	14.5
Allotype	33.3	14.0	15.3	7.4	4.9	13.8			19.0	8.9	7.1	11.0
P. (G.) cometes												
Holotype	37.3	17.1	18.5	9.2	5.6	14.5	4.9	2.0	26.8	11.1	9.6	15.8
Allotype	31.8	13.3	13.7	8.0	4.8	10.5	3.8	1.4	16.7	7.3	6.0	10.7
Morphotype	31.6	13.2	14.7	7.0	5.1	12.9	4.0	1.8	20.2	8.5	7.5	11.2
P. (G.) connus												
Holotype	35.4	17.1	14.1	6.3	4.0	14.2	4.2	1.6	25.1*	10.1*	9.0*	13.7*
Allotype	35.2	15.4	13.8	6.4	5.1	14.7	4.2	1.6	22.1	9.8	8.2	12.2
Morphotype	29.0	14.1	11.7	5.6	4.4	11.5	3.2	1.3	19.9	9.0	7.5	11.0
P. (G.) pogum												
Holotype	28.6	14.1	14.5	8.5	4.8	11.0	4.1	1.5	18.9	12.9	5.5	12.0
Allotype	36.0	15.9	17.1	8.5	5.7	14.1	4.4	1.8	19.6	8.5	7.4	11.8
Morphotype	28.4	11.7	14.1	5.4	4.4	11.6	3.1	1.4	17.0	6.7	5.8	10.9
P. (G.) h. vesticeps												
Holotype	30.3	12.6	13.4	6.5	4.7	12.6	4.1	1.7	19.8	9.1	7.7	12.2
Allotype	35.4	15.0	15.7	7.6	5.6	14.8	4.7	1.8	21.6	9.3	8.3	12.2
Morphotype	36.0			7.7	5.8	15.4	4.0	1.8	16.7	11.4	10.0	15.6

(avg. 33.70), for females was 23.9-40.0 (avg. 33.23) and 23.2-37.9 (avg. 33.28) for Form II males. Form I males had a rostrum length of 4.44-5.56 (avg. 4.82), females 4.66-6.33 (avg. 5.23) and males, Form II, 4.57-4.93 (avg. 4.73); there was significant sexual dimorphism in this characteristic. The rostrum was 1.13-1.54 (avg. 1.36) times longer than wide in Form I males; 1.10-1.36 (avg. 1.27) in females and 1.28-1.46 (avg. 1.36) in Form II males. Areola length values for Form I males were 2.24-2.50 (avg. 2.40), 2.25-2.86 (avg. 2.45) for females and 2.34-2.86 (avg. 2.52) for Form II males. The antennal scale length for Form I males was 6.30-9.11 (avg. 8.03), for females 7.47-9.41 (avg. 8.35) and 7.73-9.00 (avg. 8.31) for Form II males. As expected, sexual dimorphism existed in the characteristics of the chela. Chela length in Form I males was 1.36-1.53 (avg. 1.41), in Form II males 1.38-2.16 (avg. 1.65) and in females 1.50-2.01 (avg. 1.76); chela width was 2.18-2.65 (avg. 2.31), 1.46-2.40 (avg. 2.08) and 2.07-2.88 (avg. 2.26), respectively. Form I males had an inner palm length of 2.48-2.82 (avg. 2.60) and a dactyl length of 1.62-1.83 (avg. 1.73). In Form II males the same values were, respectively, 1.67-2.84 (avg. 2.46) and 1.07-1.72 (avg. 1.46); and in females they were 2.42-2.73 (avg. 2.57) and 1.61-1.83 (avg. 1.74). Pleopod length in Form I males was 2.18-3.67 (avg. 3.35) and 3.27-3.67 (avg. 3.48) in Form II males.

Most morphological variations are within the limits set by the types, but some discussion of the populations around Muldon, Monroe County, Mississippi, seems necessary. This is the principal population on which I base my conclusion that *vesticeps* and *hagenianus* are conspecific, despite some striking morphological differences, most obvious of which are setiferous ornamentations. In one collection (USNM 57278, 2 ♂♂I, 5 ♀♀): all of the characteristics are of *vesticeps* except that the chelae are not bearded in one male, and the lateral margin of the ischium of the third maxilliped in all specimens is poorly provided with setae. In the females the postannular sternite is flat and trapezoidal in four and has a conical protuberance in the other. In one male the central projection is enveloped basally by a fold as in *hagenianus* on one pleopod, while on the other pleopod the composition is as in *vesticeps*. In USNM 44746, of 90+ specimens, there is one female with a postannular sternite and maxilliped setation intermediate between *hagenianus* and *vesticeps;* in two the sternite is *hagenianus*-like and the maxilliped is *vesticeps*-like; in nine the sternite-maxilliped characterizations are the reverse. Among the Form I males, seven have the setation of the ischium of the maxilliped and of the mesial margin of the hand much less dense than typical *vesticeps*. The remaining specimens are within the limits of variability typical of *vesticeps*. For morphometric comparisons a total of 130 specimens (55 ♂♂I, 4 ♂♂II, 71 ♀♀) of the intergrade population were used.

Specimens examined. – MISSISSIPPI: "NE Mississippi," 10 April 1911 (4 ♂♂I, 3 ♀♀); Chickasaw Co., Egypt, no date (6 ♂♂I, 3 ♂♂II, 6 ♀♀), Okalona (7 ♂♂I, 1 ♂II); Monroe Co., Slough at jct. St. Rtes. 8 and 25, 1 April 1966 (1 ♂ imm.); Pontotoc Co., "Nr. Hurracine [= Hurricane] nr. Thaxton," 1 May 1937 (1 ♀).

Intergrades *(P. h. hagenianus* x *P. h. vesticeps).* – MISSISSIPPI: Monroe Co., Muldon, July, 1912 (3 ♂♂I, 6 ♀♀), Fall, 1922 (1 ♂II, 6 ♀♀), no date (1 ♂I), (6 ♂♂I, 1 ♀), (1 ♂I, 1 ♀), (1 ♂I, 2 ♀♀); no locality, no date (♂♂I, ♂♂II, ♀♀, 90+ specimens).

Remarks. – Lyle (1937:44-45) reported: "The writer attempted to cross this crawfish [*C. h. evansi* (=*P. h. vesticeps*)] with *C. hagenianus* but was unable to get either species to mate in captivity." One must, however, consider this in light of the fact that *none* of his attempts at laboratory mating of *any* species was successful.

Etymology. – From *vesticeps* (L.): bearded, arrived at puberty; an allusion to the setiferous bearding characteristic of the hand and maxilliped in this subspecies.

Procambarus (Girardiella) barbiger n. sp.
Figures 37 - 52

Cambarus (Girardiella) hagenianus forrestae Lyle, 1938:76, *nom. nud.*

Procambarus hagenianus. – Fitzpatrick, 1968:37 (part).

Procambarus (Girardiella) hagenianus. – Hobbs, 1972b:47 (part), 151 (part), 154 (part) (by implication).

Procambarus (Girardiella) sp. B. – Fitzpatrick, 1975:385, 386, 387, 388.

Diagnosis. – Body pigmented, eyes small but well-developed. Rostrum with gently converging margins, lacking marginal spines; acumen short, indistinctly delimited basally. Areola 38.32-43.87% of entire length of carapace (avg. 41.81); areola linear. Carapace devoid of cervical spines or tubercles. Suborbital angle obsolete. Postorbital ridges lacking spines or tubercles cephalically. Antennal scale 2.40-2.71 (avg. 2.69) times longer than wide, widest near midlength, thickened lateral portion terminating in strong, acute spine. Mesial margin of palm provided with dense setiferous beard, tubercles obscure; movable finger with small tuft of stout setae and strong tubercle distal to it on proximal fourth. Opposable margin of immovable finger with row of five prominent tubercles in proximal half, two in distal half, distal half with crowded minute denticles; opposable margin of movable finger with three stout tubercles, distal third with crowded minute denticles. Ischia of third pereiopods only with stout spine; no prominence or bosses on coxae of third through fifth pereiopods. Inner ramus of uropod with two conspicuous spines protruding beyond distal margin. First pleopods symmetrical, shoulder present at base of central projection; pleopods reaching caudal margin of coxae of third pereiopods when abdomen flexed; distal extremity bearing (1) prominent, subacute mesial process directed distally and slightly mesially, extending distally beyond other terminal elements; (2) well-developed central projection with apical portion bent slightly mesially, centrocephalic process enveloped at base by fold continuous with centro-caudal process; and (3) conspicuous, well-developed, subtriangular (in lateral aspect) caudal process extending distally subparallel to central projection for 80% of length of central projection, caudodistal margin lamelliform. Annulus ventralis of female very deeply excavate cephalically with strong cephalolateral ridges terminating (ventrally) in three to four tubercles and set off cephalically by groove; deep sinus originating in sulcus near center of annulus and describing gentle arc to caudal margin; postannular sternite in shape of triangular prism.

Holotypic male, Form I. – Body subovate, distinctly compressed. Abdomen narrower than thorax (11.6 and 16.1 mm). Width of carapace at caudodorsal margin of cervical groove less than height (16.1, 19.0 mm). Areola 42.38% of total length of carapace and linear; cephalic section of carapace 1.4 times as long as areola (Fig. 39). Rostrum sharply depressed (Fig. 43), deeply excavate dorsally, with thickened lateral margins slightly converging cephalically, marginal spines lacking, acumen indistinctly delimited basally; upper surface sparsely punctate, usual submarginal row of setiferous punctations present. Subrostral ridges moderately well-developed to level of suborbital angle and visible in dorsal aspect to midlength of rostrum. Branchiostegal spine small but acute. Carapace punctate dorsally and laterally; granulate cephalolaterally with granules best developed just posterior to suborbital angle. Cervical spines or tubercles absent. Cephalic section of telson with two spines in each caudolateral corner (Fig. 51). Cephalic portion of epistome subtriangular in outline, about as broad as long, lacking

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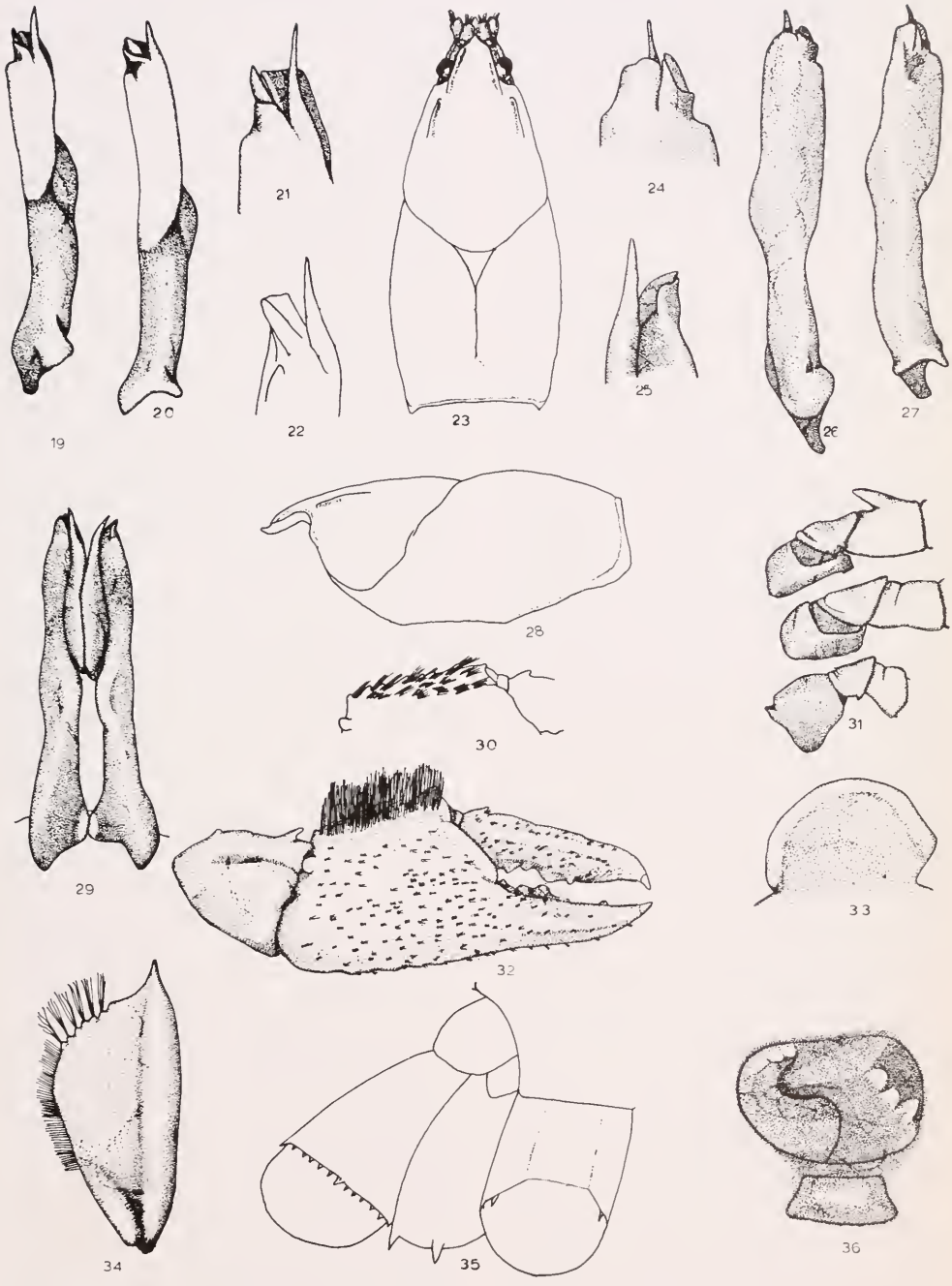
Figures 19-36. *Procambarus (Girardiella) hagenianus vesticeps* n. subsp.: 19, mesial view of first pleopod of holotypic male, Form I; 20, mesial view of first pleopod of morphotypic male, Form II; 21, terminal elements of first pleopod of holotype, mesial view; 22, terminal elements of first pleopod of holotype, cephalic view; 23, dorsal view of carapace of holotype; 24, terminal elements of first pleopod of holotype, lateral view; 25, terminal elements of first pleopod of holotype, caudal view; 26, lateral view of first pleopod of morphotype; 27, lateral view of first pleopod of holotype; 28, lateral view of carapace of holotype; 29, caudal view of first pleopods of paratypic Form I male; 30, mesial margin of palm of allotype; 31, proximal podomeres of third through fifth pereiopods of holotype; 32, distal podomeres of cheliped of topoparatypic Form I male; 33, cephalic portion of epistome of holotype; 34, antennal scale of holotype; 35, telson and left uropod of holotype; 36, annulus ventralis and postannular sternite of allotype.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cephalomedian tubercle (Fig. 41). Antennules of usual form with well-developed spine on ventral surface of basal segment slightly distal to midlength. Antennae broken, but seemingly reaching to about caudal margin of carapace; antennal scale (Fig. 50) 2.4 times longer than wide, broadest approximately at midlength; thickened lateral portion terminating cephalically in strong acute spine about 18% of total length of scale.

Ischium of third maxilliped with long, stiff, dense setae arising from mesial and ventrolateral margins.

Right chela (Fig. 49) with palm inflated, moderately depressed; lateral margin nearly straight, not costate; entire palmar area covered with setiferous punctations; mesial margin of palm with mat of dense long setae obscuring tubercles; row of four squamous setiferous tubercles median to setal prominences; mesial margin of movable finger with tuft of setae in proximal fourth, prominent tubercle in proximal third distal to tuft of setae. Opposable margin of movable finger slightly excavate in basal third; with three stout tubercles in basal half, finger excavate in same region; three small tubercles distal to prominent tubercles and crowded minute denticles in distal fourth. Opposable margin of immovable finger with row of two small, one large, two small tubercles in basal half, one only in basal fourth; distal half with crowded minute denticles and with two small tubercles, one at origin of denticles, second halfway to tip. Both fingers with submedian longitudinal ridge above and below flanked by setiferous punctations. Lower surface of palm sparsely punctate with few tubercles in distal portion.

Carpus of right cheliped longer than broad with mesial margin bearing two strong spines near midlength and two spinose tubercles in mesiodistal fourth; punctate dorsally with longitudinal furrow slightly mesial to midline; lower distal margin with spine in each corner, third spine halfway between mesiodistal spine and aforementioned stout mesial spines.

Merus of right cheliped with dorsomedian row of 14 spines, distal three acute, remainder low and rounded, almost tubercular; ventral surface with mesial row of 11 irregularly spaced acute spines, stoutest distalmost, and lateral row of seven irregularly spaced spines, distalmost stoutest. Ischium with mesial row of two spines.

Hooks on ischia of third pereiopods only; hooks simple, directed proximally, projecting proximad to midlength of basis (Fig. 48). Coxae of third, fourth and fifth pereiopods lacking prominences or bosses.

First pleopods (Figs. 37, 38, 40, 42, 45, 47) as described in *"Diagnosis"*; central projection corneous.

Uropods (Fig. 51) with mesial ramus bearing two subequal spines projecting beyond caudal margin, one from lateral corner and one from median ridge. Sternites and coxae of all pereiopods, especially in pereiopodal segments II-V, bearing setae partially concealing pleopods when latter held under thorax.

Male, Form II. – Unknown.

Allotypic female. – Differing from holotype in following respects: areola 41.44% of entire carapace length; left antennal scale (Fig. 44) with two stout flat spines originating from middle of mesial margin of lamellar portion and mesiodistal margin of antennal scale. Mesial margin of palm (Fig. 46) with mesial row of seven setiferous squamous tubercles, row of six dorsomedial to them and irregularly spaced squamous setiferous tubercles over much of mesial half of upper surface; chelae proportionately shorter and less inflated; setiferous beard of ischia of third maxillipeds not as dense; pereiopodal sternites essentially lacking concealing setae.

Annulus ventralis (Fig. 52) deeply excavate cephalically with strong cephalolateral prominences extending (ventrally) one and one-half times depth of remainder of annulus, left terminating (ventrally) in two large and two small tubercles, right in three subequal tubercles; sinus originating near center of annulus, curving gently sinistrad to caudal margin; annulus delimited cephalically by groove. Postannular sternite as described in *"Diagnosis."*

Types. – USNM nos. 146258 (holotype) and 146259 (allotype); *Paratypes:* Missis-

sippi, Scott County (4 ♂♂I, 11 ♀♀).

Type-locality. – Forrest, Scott County, Mississippi.

Range. – This species is known only from burrows in and about Forrest, Scott Co., Mississippi, but probably occurs throughout the band of Jackson Prairie running southeastward from central Mississippi through Rankin, Scott, Smith, Newton, Jasper, Clarke and Wayne counties and possibly Madison and Hinds counties. All of the known specimens were collected from the environs of Forrest, and I have never been able to collect the species personally despite repeated efforts. I have, however, attempted the excavation of burrows which were probably made by this species near Forrest, and the environmental situation in which these burrows occurred was nearly identical with that in which *P. hagenianus* is found– large open fields relatively remote from watercourses. Lyle (1937:48) recorded the species (as *P. h. forrestae)* from "Leesburg, Rankin County," but I have been unable to locate the specimens on which this record is based. The only "Rankin" specimens I have seen are USNM no. 93101 ("near Jackson [Hinds or Rankin Co.], leg. Carlysle Carr, May, 1936") which are unquestionably assignable to *P. h. hagenianus.* Mr. Carr, an employee of the U. S. Biological Survey, worked intimately with the state Fish and Wildlife Service, and I believe that the locality appearing on the label of these specimens reflects that the specimens were received from Jackson, on the site of the Fish and Wildlife Service Museum. I offer in support of this thesis the fact that no other specimens resembling the subspecies have been collected or reported from the vicinity of Jackson.

Color. – I have never seen fresh specimens personally, but Lyle (1937:48) gives a limited description: "color is rather variable but blue apparently predominates."

Variation. – Most of the limits of variation are within the limits set by the primary types, but in a collection of two females (USNM no. 146273) one specimen is typical of *barbiger,* and the other lacks the hirsute ornamentation of the mesial portion of the palm; furthermore the annulus is not typical. Neither specimen possesses the lateral row of dense setae on the ischium of the third maxilliped, but both have a postannular sternite characteristic of *barbiger.* In the topotypic series (4 ♂♂I, 9 ♀♀), one female has a dextrally oriented sinus and less prominent tubercles on the annulus than the rest of the specimens; in another female the tubercles are placed much more cephalomesially than the rest; in a third specimen the tubercles are broad, prominent and lateral; and in a fourth the tubercular prominences seem almost montane in comparison. The shoulder on the cephalic surface of the first pleopod of one male is much more sharply angular than in the remaining specimens.

Morphometric analysis was based on 15 specimens (4 ♂♂I, 11 ♀♀). Carapace length was 24.0-36.1 (avg. 29.15) in Form I males and 28.5-36.3 (avg. 32.17) in females. In males, Form I, rostrum length was 3.87-4.51 (avg. 4.27) and 4.16-5.00 (avg. 4.48) in females. The rostrum was 1.29-1.55 (avg. 1.45) times longer than wide in Form I males and 1.16-1.76 (avg. 1.43) in females. The areola length was 2.36-2.43 (avg. 2.39) in Form I males and 1.77-2.61 (avg. 2.42) in females. Antennal scale values were available only for females, and they were 7.68-7.80 (avg. 7.74) for length and 2.67-2.71 (avg. 2.69) for width. Chela length was 1.47-1.50 (avg. 1.48) in Form I males and 1.69-1.84 (avg. 1.77) in females. Chela width was 2.17-2.40 (avg. 2.28) in Form I males and 2.03-2.15 (avg. 2.09) in females. In Form I males length of the mesial margin of the palm and dactyl length were, respectively, 2.67-2.80 (avg. 2.75) and 1.66-1.72 (avg. 1.69), while the same two characters in females were 2.06-2.68 (avg. 2.46) and 1.61-1.73 (avg. 1.67). Pleopod length in the Form I males was 3.08-3.84 (avg. 3.44).

Specimens examined. – MISSISSIPPI: Scott Co., Forrest, 2 May 1936 (4 ♂♂I, 9 ♀♀), March, 1934 (2 ♀♀).

Remarks. – In the topotypic series, collected 2 May 1936, three of the nine females had a sperm plug in the annulus ventralis.

Etymology. – From *barbiger* (L.): wearing a beard; so named because of the hirsute

nature of the mesial margin of the hand in both sexes and the bearding of the ischium of the third maxilliped.

Procambarus (Girardiella) cometes n. sp.
Figures 53 - 71

Procambarus (Girardiella) hagenianus. – Hobbs, 1972b:47 (part), 151 (part), 154 (part) (by implication).

Procambarus (Girardiella) sp. E. – Fitzpatrick, 1975:385, 386, 387, 388.

Diagnosis. – Body pigmented, eyes small but well-developed. Rostrum with slightly converging margins, lacking marginal spines; acumen short and indistinctly delimited basally. Areola linear and 38.77-43.24 (avg. 40.01)% of total length of carapace. Carapace devoid of cervical spines or tubercles. Suborbital angle absent. Postorbital ridges without spines or tubercles. Antennal scale 2.33-2.87 (avg. 2.51) times longer than wide, broadest near midlength, thickened lateral portion terminating cephalically in long, acute, stout spine. Mesial margin of palm with surface obscured by dense mat of setae in first form male, second form male with numerous tufts of short stiff setiferous bristles, female with single row of five or six tubercles and sparse setiferous squamous tubercles; basal portion of movable finger excavate along opposable margin with row of five or six tubercles in basal two-thirds; opposable margin of immovable finger with row of seven or eight tubercles in basal two-thirds and single tubercle at base of distal fourth. Ischia of third pereiopods only bearing simple hooks; coxae of third, fourth and fifth pereiopods lacking prominences or bosses. Inner ramus of uropod with two conspicuous spines projecting distally beyond margin. First pleopods symmetrical, reaching caudal margin of coxa of third pereiopod when abdomen flexed; small shoulder present at base of central projection; distal extremity bearing (1) prominent central projection directed more or less laterodistally (2) subacute mesial process directed laterodistally, projecting only slightly beyond tips of other elements; and (3) subrhomboidal (in lateral aspect) caudal process excavate mesially, lamelliform in caudodistal half. Annulus ventralis of female deeply excavate cephalically with prominent cephalolateral ridges terminating (ventrally) in tubercles, sulcus relatively narrow (only 20-25% width of annulus), annulus set off cephalically by shallow groove; sinus originating near center of annulus and passing in gentle arc to caudal margin; postannular sternite subconical in shape.

Holotypic male, Form I. – Body subovate, distinctly compressed. Abdomen narrower than carapace (13.3 and 17.1 mm). Carapace higher than wide at caudodorsal margin of cervical groove (18.5, 17.1 mm). Areola 38.87% of total length of carapace and linear (Fig. 57). Cephalic section of carapace 1.6 times as long as areola. Rostrum slightly depressed (Fig. 62), deeply excavate dorsally with thickened lateral margins gently convergent distally, marginal spines lacking, acumen indistinctly delimited basally; upper surface sparsely punctate, usual row of submarginal setiferous punctations present. Subrostral ridges moderately well-developed from suborbital level and visible to about midlength of rostrum in dorsal aspect. Postorbital ridges moderately prominent, grooved dorsolaterally, and terminating cephalically without spines or tubercles. Suborbital angle lacking. Branchiostegal spine reduced. Carapace very sparsely punctate but with squamous tubercules laterally, tubercles most numerous in cephaloventral portion. Cervical spines or tubercles absent. Telson (Fig. 70) divided with two spines in right caudolateral corner and three in left. Cephalic portion of epistome (Fig. 68) about as broad as long with tubercular mesiocephalic projection. Antennules of usual form with well-developed spine on ventral surface of basal segment slightly distal to midlength. Antennae extending about to caudal margin of carapace; antennal scale (Fig. 69) 1.57 times longer than wide, broadest distal to midlength, thickened lateral portion terminating cephalically in strong acute spine approximately 23% of total length of antennal scale, cephalic margin of lamellar portion provided with relatively few tubercular eminences bearing tufts of setae.

Ischium of third maxilliped with prominent, stiff, simple, unmatted setae running along entire mesial and ventrolateral margin.

Right chela (Fig. 67) with palm inflated, not strongly depressed; lateral margin not costate; upper and lower surfaces punctate except along mesial margin; mesial margin of palm almost devoid of tubercles but provided with dense mat of long, stiff setae; setae in distinct tufts arising from large, deep punctations. Opposable margin of fixed finger with row of three small, one large, and three small tubercles in basal two-thirds, single large tubercle directed ventromesially from base of distal fourth, distalmost 10% broken, but with crowded minute denticles distal from tubercle; submedian longitudinal ridge flanked by setiferous punctations above. Opposable margin of dactyl excavate in basal half with row of three small, one large and two small tubercles along basal two-thirds, crowded minute denticles in distal fourth; mesial margin with two evenly spaced setiferous tubercles in basal fourth; submedian longitudinal ridge above flanked by setiferous punctations.

Carpus of right cheliped longer than wide, with mesial margin bearing stout acute spine in distal fourth, small acute spine in mesiodistal corner; remainder of upper surface punctate, but with longitudinal furrow in distalmost three-fourths; lower surface with strong acute spines in each distalmost corner. Merus of right cheliped with row of ten tubercles on upper surface and two acute spines terminating row distally; lower surface with mesial row of 14 acute spines increasing in size distally, and lateral row of nine smaller acute spines likewise increasing in size distally. Ischium with mesial row of two small tubercles.

Hooks on ischia of third pereiopods only (Fig. 65); hooks simple, directed proximally and projecting proximally to distal fourth of basis. Coxae of third, fourth and fifth pereiopods lacking prominences or bosses.

First pleopods symmetrical and as described in *"Diagnosis"*; central projection and caudal process corneous (Fig. 53, 55, 56, 58, 59, 61, 66).

Uropods (Fig. 70) with mesial ramus bearing two spines projecting beyond caudal margin, one from lateral corner, and other, slightly longer, from median ridge.

Sternum between coxae of second through fifth pereiopodal segments slightly excavate, lateral margins bearing sparse tufts of setae only partially obscuring first pair of pleopods when pleopods held beneath thorax.

Morphotypic male, Form II. – Differing from holotype in following respects: dorsal punctation of carapace present; tip of immovable finger of chela unbroken and crowded minute denticles occurring to level of corneous acute tip; mesial margin of palm (Fig. 63) lacking dense bearding, but provided with numerous tufts of shorter setae clearly arising from deep large setiferous punctations; carpus of cheliped bearing small acute spine between mesial spine and ventromesial spine on both chelipeds. First pleopods (Figs. 54, 60) with tips non-corneous, proportionally less developed, and central projection with fold at base wrapping around mesial, cephalic and lateral portions, mesial process extending proportionately farther beyond tip of other elements. Only two spines in left caudolateral margin of cephalic portion of telson. Hooks on ischia of third pereiopods much less pronounced than in holotype.

Allotypic female. – Differing from holotype in following respects: cephalic portion of epistome subtrapezoidal and broader than long; areolar region with transverse crease *pre-mortem* injury and only 33.02% of total length of carapace; mesial margin of chela (Fig. 64) lacking beard, bearing instead five tubercles, some of which provided with quite light setiferous tufts; distalmost portion of immovable finger similar to that of morphotype; small acute spine between spine and ventrodistal spine of carpus as in morphotype.

Annulus ventralis (Fig. 71) about as broad as long, with deep subtrapezoidal excavation in centrocephalic portion, cephalolateral margins markedly raised (ventrally) with three tubercles on left ventralmost margin and four on right; sinus originating near center, forming arc sinistrally and be-

coming lost in caudal margin near midline; postannular sternite subconical in shape.

Types. – USNM nos. 130227, 146260, and 131280 (holo-, allo-, and morphotype, respectively); *Paratypes:* Oktibbeha (2 ♂♂I, 9 ♀♀) and Lowndes (1 ♂I) counties, Mississippi.

Type-locality. – Field behind Luxury Mobile Homes (T18N, R14E, SW¼, Sec. 3), Starkville, Oktibbeha County, Mississippi.

Range. – The species is known from only two localities in Oktibbeha County (the type locality and 8.8 mi S of Starkville, jct. St. Rte. 25, on St. Rte. 12) and one in Lowndes County (6.6 mi E of Old State Route 12 in Starkville). It seems to be associated with the Flatwoods belt in Oktibbeha Co., but the specimen from Lowndes Co. came from the Black Belt.

Color. – *P. cometes* resembles *P. hagenianus* in color–dark blue ground color with cream markings–but I have never seen a "red" phase. This species was unknown to Lyle, therefore he left no color notes.

Variation. – Most of the limits of variation are incorporated in the diagnosis and descriptions above. In four female specimens from south of Starkville (USNM no. 146274), the mesial margin of the hands is provided with sparse, widely scattered tufts of setae not markedly different from the condition found in *P. barbiger;* an associated Form I male is typical of the species. The extremely short areola (comparatively) of the allotype seems to be unique.

Morphometric variation analysis is based on 14 specimens (4 ♂♂I, 10 ♀♀). Carapace length in males was 29.6-37.3 (avg. 33.30) and 31.8-40.7 (avg. 35.54) in females. In males the rostrum length was 4.05-4.63 (avg. 4.24) and in females 3.98-4.69 (avg. 4.35), while rostrum width values were 1.33-1.66 (avg. 1.54) and 1.34-1.67 (avg. 1.46), respectively. Areola length was 2.45-2.58 (avg. 2.54) in males and 2.31-3.03 (avg. 2.54) in females. Antennal scale length was 7.65-8.05 (avg. 7.75) in males and 7.39-8.85 (avg. 8.12) in females. Chela length in males was 1.39-1.66 (avg. 1.51) and in females was 1.71-1.92 (avg. 1.81); chela width was 2.23-2.46 (avg. 2.34) in males and 2.05-2.47 (avg. 2.26) in females. Length of the mesial margin of the palm and length of the dactyl were, respectively, in males 2.79-2.97 (avg. 2.88) and 1.52-1.70 (avg. 1.64); in females the same characters in the same sequence were 2.59-3.01 (avg. 2.77) and 1.56-1.90 (avg. 1.66). Pleopod length in males was 3.65-3.89 (avg. 3.72).

Specimens examined. – MISSISSIPPI: Lowndes Co., 6.6 mi. E of Starkville, 12 July 1968 (1 ♂I); Oktibbeha Co., Luxury Mobile Homes (T18N, R14E, SW¼ Sec. 3), Starkville, no date (1 ♀), (1 ♂I, 1 ♀), (1 ♂I), (1 ♀), (3 ♀♀), 8.8 mi. S of Starkville on St. Rte. 12, no date (1 ♂I, 4 ♀♀).

Etymology. – From *cometes* (L.): one with long hair; used with reference to the long setae on the mesial margin of the palm of males and the long setae on the ischium of the third maxilliped.

Procambarus (Girardiella) connus n. sp.
Figures 72 - 90

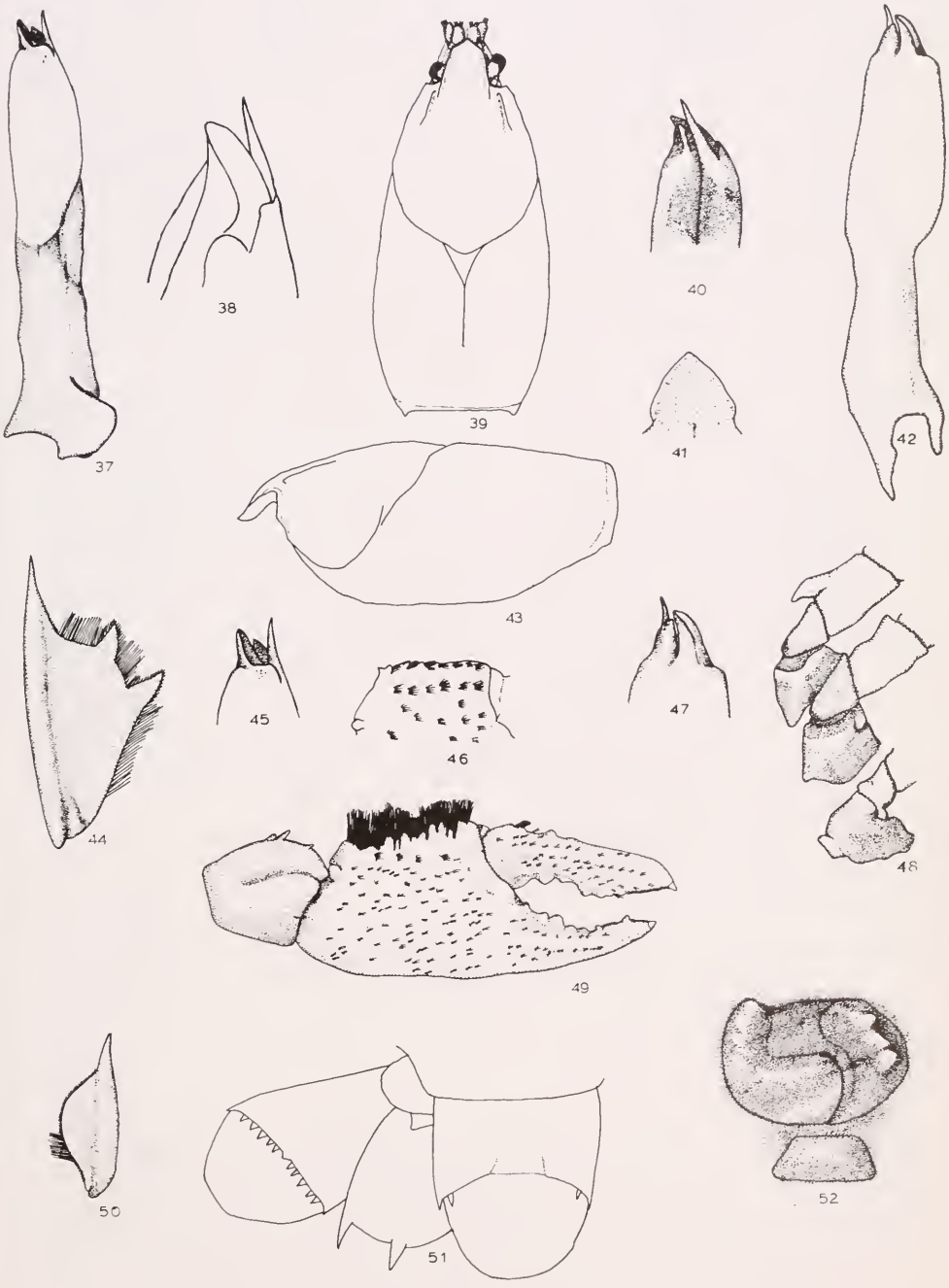
Procambarus hagenianus. – Fitzpatrick, 1968:37 (part).

Procambarus (Girardiella) hagenianus. – Hobbs, 1972b:47 (part), 151 (part), 154 (part) (by implication).

Procambarus (Girardiella) sp. C. – Fitzpatrick, 1975:385, 386, 387, 388.

Diagnosis. – Body pigmented, eyes small but well-developed. Rostrum with gently

Figures 37-52. *Procambarus (Girardiella) barbiger* n. sp.: 37, mesial view of first pleopod of holotypic male, Form I; 38, teminal elements of first pleopod of holotype, cephalic view; 39, dorsal view of carapace of holotype; 40, terminal elements of first pleopod of holotype, caudal view; 41, cephalic portion of epistome of holotype; 42, lateral view of first pleopod of holotype; 43, lateral view of carapace of holotype; 44, left antennal scale of paratypic female; 45, terminal elements of first pleopod of holotype, mesial view; 46, mesial margin of palm of allotype; 47, terminal elements of first pleopod of holotype, lateral view; 48, proximal podomeres of third through fifth pereiopods of holotype; 49, distal podomeres of cheliped of holotype; 50, antennal scale of holotype; 51, telson and left uropod of holotype; 52, annulus ventralis and postannular sternite of allotype.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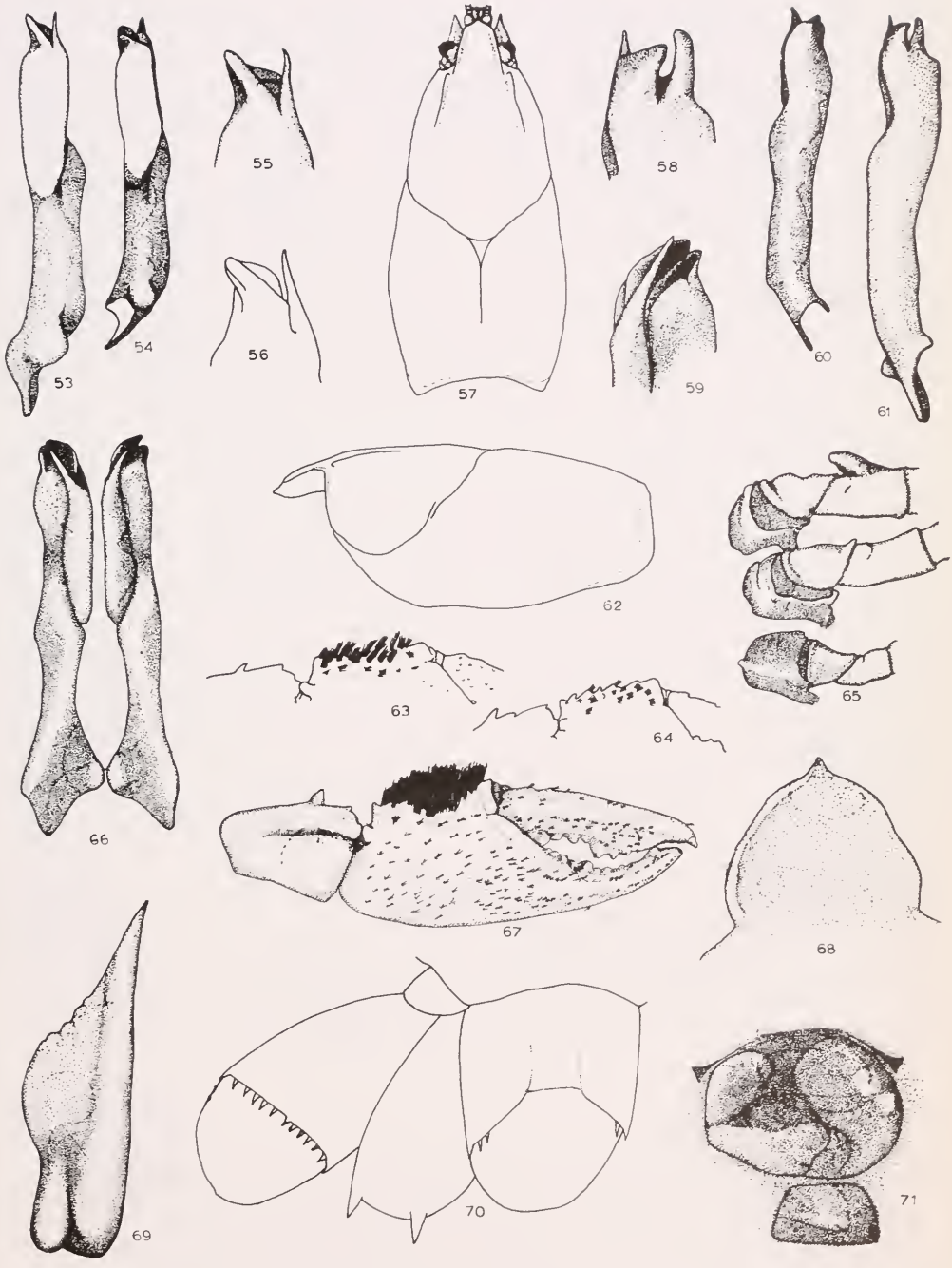
converging margins, lacking marginal spines, acumen short and indistinctly delimited basally. Areola constituting 38.39-44.79 (avg. 41.41)% of total length of carapace; areola linear. Carapace devoid of cervical spines or tubercles. Suborbital angle obsolete. Postorbital ridges without spines or tubercles. Antennal scale 2.00-2.88 (avg. 2.44) times longer than wide, thickened lateral portion terminating cephalically in stout, comparatively short spine, broadest slightly distal to midlength. Mesial margin of palm with setiferous mat of hairs obscuring tubercular ornamentation. Opposable margin of immovable finger with row of eight tubercles in basal three-fourths, third from base largest; opposable margin of dactyl slightly excavated in basal third, with row of seven tubercles, first and fourth larger than remainder. Ischia of third pereiopods only bearing simple hooks; coxae of third, fourth and fifth pereiopods lacking prominences or bosses. Inner ramus of uropod with two conspicuous spines projecting distally beyond margin. First pleopods very slightly asymmetrical, slight shoulder at base of central projection; distal extremity bearing (1) prominent central projection directed laterodistally, tightly applied fold continuous with centrocaudal process enveloping base of centro-cephalic process; (2) subacute mesial process directed caudal subparallel to main axis of shaft, extending length of central projection beyond other terminal elements; and (3) subrectangular (in lateral aspect) caudal process subparallel to mesial plane of pleopod with caudodistal margin lamelliform. Female with rather simple (in comparison with relatives) annulus ventralis; annulus deeply excavate in centrocephalic portion with prominent lateral prominences (ventrally), prominences lacking tubercular ornamentation; annulus set off cephalically by groove; sinus originating slightly anterior to center of structure, curving sinistrally to be lost in caudal fourth; postannular sternite subrhomboid in outline, not highly elevated.

Holotypic male, Form I. — Body subovate, distinctly compressed. Abdomen narrower than carapace (10.3 and 17.1 mm). Width of carapace at caudodorsal margin of cervical groove greater than height (17.1, 14.1 mm). Areola 41.24% of total length of carapace; areola linear (Fig. 76). Cephalic section of carapace 1.4 times as long as areola; rostrum depressed, deeply excavated dorsally, with gently converging thickened lateral margins, marginal spines lacking, acumen indistinctly delimited basally; upper surface not punctate except for usual submarginal row of setiferous punctations. Subrostral ridges moderately well-developed from level of suborbital angle and visible dorsally to approximately midlength of rostrum. Postorbital ridges moderately well developed, grooved cephalolaterally, terminating cephalically without spines or tubercles. Suborbital angle obsolete (Fig. 81). Branchiostegal spine small, but acute. Carapace very sparsely punctate dorsally but with squamous tubercles on cephalolateral portion. Cervical spines or tubercles absent. Cephalic section of telson (Fig. 88) with three spines in right caudolateral corner and two in left. Cephalic portion of epistome (Fig. 90) subovate in outline, lacking tuber-

Figures 53-71. *Procambarus (Girardiella) cometes* n. sp.: 53, mesial view of first pleopod of holotypic male, Form I; 54, mesial view of first pleopod of morphotypic male, Form II; 55, terminal elements of first pleopod of holotype, mesial view; 56, terminal elements of first pleopod of holotype, cephalic view; 57, dorsal view of carapace of holotype; 58, terminal elements of first pleopod of holotype, lateral view; 59, terminal elements of first pleopod of holotype, caudal view; 60, lateral view of first pleopod of morphotype; 61, lateral view of first pleopod of holotype; 62, lateral view of carapace of holotype; 63, mesial margin of palm of morphotype; 64, mesial margin of palm of allotype; 65, proximal podomeres of third through fifth pereiopods of holotype; 66, caudal view of first pleopods of holotype; 67, distal podomeres of cheliped of holotype; 68, cephalic portion of epistome of holotype; 69, antennal scale of holotype; 70, telson and left uropod of holotype; 71, annulus ventralis and postannular sternite of allotype.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cular median protrusion. Antennules of usual form with well-developed spine on ventral surface of basal segment slightly distal to midlength. Antennae extending caudad approximately to caudal margin of carapace. Antennal scale (Fig. 83) 2.07 times longer than wide, widest slightly distal to midlength, thickened lateral portion terminating cephalically in very stout spine approximately 21% of total length of antennal scale; cephalic half of margin of mesial lamellar portion provided with numerous tubercular eminences bearing tufts of setae.

Ischium of third maxilliped with prominent simple, stiff, unmatted setae along mesial and ventrolateral margins.

Right chela (Fig. 85) with palm inflated, not strongly depressed; lateral margin not costate; entire palmar area covered with setiferous punctations; mesial margin with row of five prominent tubercles and second row of four above, both rows nearly obscured by beard of setae in tufts arising from deep punctations. Opposable margin of immovable finger excavate in basal third; with row of three small, one large and three small tubercles in basal two-thirds, another tubercle at level of basal fourth, except for aforementioned tubercle distal one-third with crowded minute denticles; finger with submedian longitudinal ridge above and below, both flanked by setiferous punctations. Opposable margin of dactyl with row of one large, two small, one large and three small tubercles in basal two-thirds, with crowded minute denticles beginning just distal to penultimate tubercle and extending to tip of finger, slightly excavate in proximal third; mesial margin with two tubercles in basal one-fourth (distalmost largest); submedian longitudinal ridge above, and less distinct one below, both flanked by setiferous punctations.

Carpus of right cheliped longer than broad; with mesial margin bearing stout acute spine at base of distal third, two small but acute spines, equally spaced, proximal to aforementioned spine, upper mesiodistal margin and corner with three small spines; longitudinal groove above; small acute spine in each ventrodistal corner with row of two acute spines between mesiodistal spine and stout spine of medial surface.

Merus of right cheliped with two stout spines on upper surface near distal margin; mesioventral margin with row of 12 acute spines, distalmost largest, and ventrolateral margin with row of six, increasing in size distally. Ischium with mesial row of three acute spines.

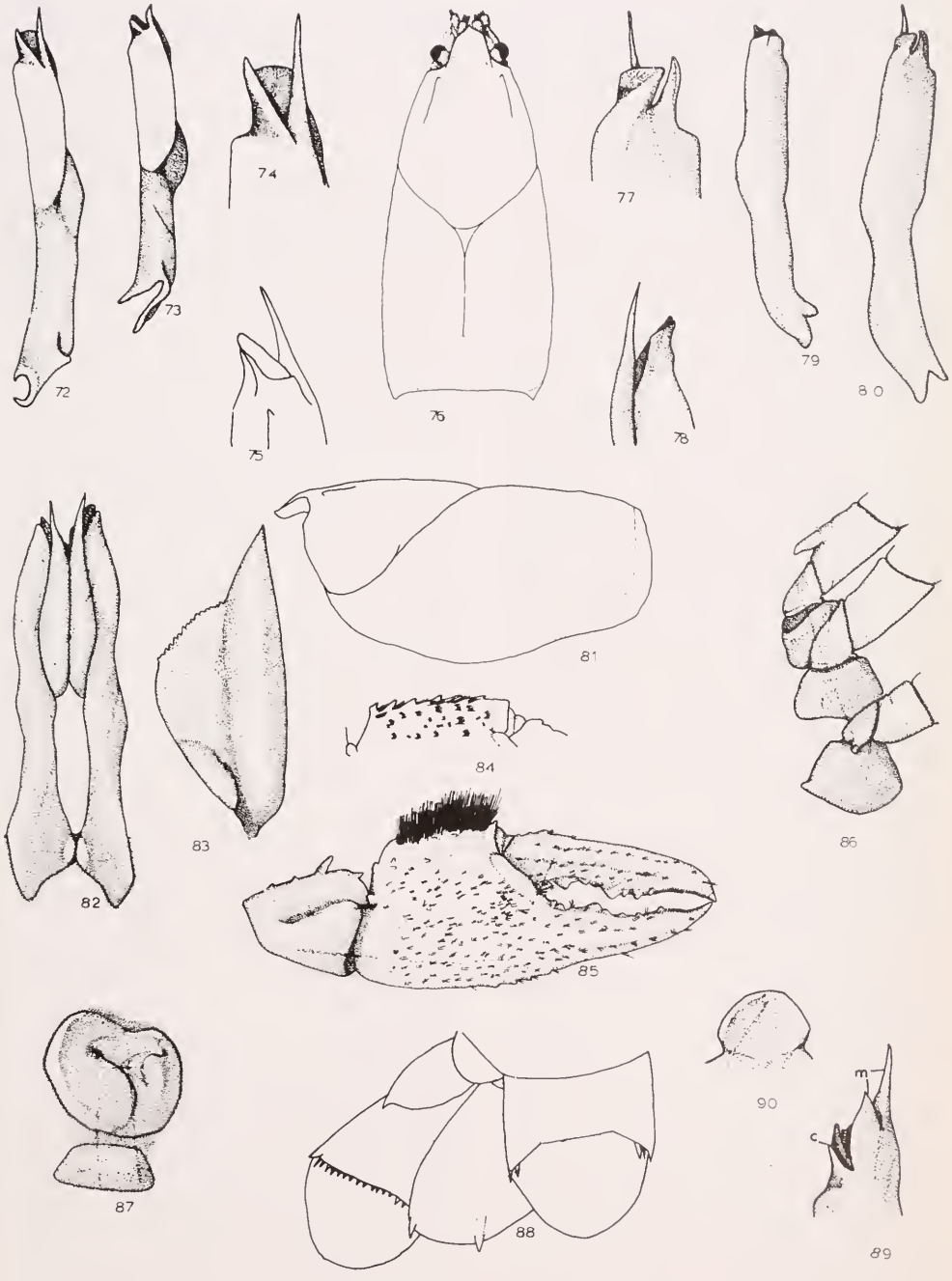
Hooks on ischia of third pereiopods only (Fig. 86); hooks simple, directed proximally and projecting to about midlength of basis. Coxae of third, fourth and fifth pereiopods lacking prominences or bosses.

First pleopods (Fig. 72, 74, 75, 77, 78, 80, 82) slightly asymmetrical and as described in *"Diagnosis"*: central projection and caudal process corneous.

Uropod (Fig. 88) with protopodite with small acute spine; mesial ramus with two spines projecting beyond distal margin, one from lateral angle and second of approximately same size from median ridge.

Sternum between third, fourth and fifth

Figures 72-90. *Procambarus (Girardiella) conmus* n. sp.:72, mesial view of first pleopod of holotypic male, Form I; 73, terminal elements of first pleopod of morphotypic male, Form II; 74, terminal elements of first pleopod of holotype, mesial view; 75, terminal elements of first pleopod of holotype, cephalic view; 76, dorsal view of carapace of holotype; 77, terminal elements of first pleopod of holotype, lateral view; 78, terminal elements of first pleopod of holotype, caudal view; 79, lateral view of first pleopod of morphotype; 80, lateral view of first pleopod of holotype; 81, lateral view of carapace of holotype; 82, caudal view of first pleopods of holotype; 83, antennal scale of holotype; 84, mesial margin of palm of allotype; 85, distal podomeres of cheliped of holotype; 86, proximal podomeres of third through fifth pereiopods of holotype; 87, annulus ventralis and postannular sternite of allotype; 88, telson and left uropod of holotype; 89, mesial view of aberrant terminal elements of paratypic male, Form I (c = central projection, m = mesial process); 90, cephalic portion of epistome of holotype.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pereiopods moderately deep and bearing long setae partially obscuring first pleopod when held under thorax.

Morphotypic male, Form II. – Differing from holotype in following respects: mesial margin of left cheliped not so densely bearded as holotype; carpus of cheliped with additional spine along mesial margin (three total); right cheliped lacking beard, with only three tubercles in mesial row on margin of palm; latter apparently regenerated; cephalic portion of telson with only two spines in right caudolateral corner. Terminal elements of first pleopod (Fig. 73, 79) not corneous and less prominent than in holotype. Hooks of ischia of third pereiopods reduced markedly, almost tubercles.

Allotypic female. – Differing from holotype in following respects: mesial margin of palm (Fig. 84) with mesial row of seven spiniform tubercles and second, more median row of six squamous tubercles, margin provided with several squamous setiferous tubercles but no beard evident. Cephalic section of telson with only two spines in right caudolateral corner; sternites associated with third to fifth pereiopods not so deeply excavate, likewise, setae much reduced.

Annulus ventralis (Fig. 87) with broad centrocephalic excavation and set off cephalically by groove; prominent, but smooth cephalolateral ridges rising (ventrally) above sulcus, right continuing as lower ridge to midcaudal line; sinus originating cephalolateral to midline and arcing sinistrally to be lost in caudal fourth of annulus. Postannular sternite subtrapezoidal in outline and not highly elevated.

Types. – USNM nos. 146261, 146262, and 146263 (holo-, allo, and morphotype, respectively); *Paratypes:* Carroll County, Mississippi (47 ♂♂I). Paratypes at USNM.

Type-locality. – Carrollton, Carroll County, Mississippi.

Range. – *P. connus* is known only from the environs of Carrollton, Carroll County, Mississippi. This species is the only member of this group found associated with loess, being located in an area of brown loam and thick loess. Although Carrollton is in the Red Hills, remnants of the mantle do occur in the vicinity, too close to be ignored.

Color. – No color records for this species exist.

Variation. – Morphometric analysis was based on 44 Form I males. Carapace length was 26.6-41.0 (avg. 34.15). Rostrum length was 3.45-6.34 (avg. 5.31) and width was 1.08-1.58 (avg. 1.38). The length of the areola was 1.71-2.57 (avg. 2.40) and the length of the antennal scale was 6.05-9.31 (avg. 8.24). Chela length was 0.99-1.47 (avg. 1.37) and chela width was 2.09-2.59 (avg. 2.35). Length of the mesial margin of the palm and length of the dactyl were 2.38-2.82 (avg. 2.63) and 1.40-4.65 (avg. 1.81), respectively. Pleopod length was 2.51-3.84 (avg. 3.35).

In the topotypic series, one male of 17 had the mesial margin of the palm of the left cheliped almost devoid of setae; the right cheliped of this specimen and all the remaining specimens were like the holotype. In a second paratypic collection, one of 14 males had both chelipeds devoid of setiferous ornamentation (thus resembling *hagenianus*), and the ischia of the third maxillipeds were likewise devoid of dense setiferous beards. In the third paratypic series one of 17 males had a clearly regenerated hand which was lacking the beard of the inner margin of the palm; two had a straight mesial process. Otherwise, variation fell within the limits established in the diagnosis and descriptions outlined above. In one male, Form I, the terminal elements of the left first pleopod were markedly aberrant (Fig. 89); whether or not this was the result of an injury could not be ascertained.

Specimens examined. – MISSISSIPPI: Carroll Co., Carrollton, no date (17 ♂♂I, 1 ♂II, 1 ♀), (14 ♂♂I), (17 ♂♂I).

Remarks. – *P. connus* seems almost as closely related to *P. h. hagenianus* as is *P. h. vesticeps*. Indeed, I would say as closely were it not for the fact that apparent intergrade populations exist between the latter two. I find no suggestion that a zone of intergradation exists between *P. hagenianus* and *P. connus*. Therefore, I have taken the more conservative position, designating *connus* a species. Should intergrade populations be discovered subsequently, a minor

nomenclatorial change will rectify the situation. Although the degree of relationship existing between *P. h. hagenianus, P. h. vesticeps* and *P. connus* is not as precisely delimited as one might wish, each population represents a morphologically and geographically distinct entity as indicated more thoroughly in the "Discussion" section following.

Etymology. – The name of this species is taken from *konnos* (Gr.): a beard: this is in reference to the bearding of the mesial margin of the palm in males and the bearding of the third maxilliped.

Procambarus (Girardiella) pogum n. sp.
Figures 91-108

Cambarus (Girardiella) hagenianus carri Lyle, 1938:76, *nom. nud.*

Procambarus hagenianus. – Hobbs, 1968:K25 (Fig. 19c); Fitzpatrick, 1968:37 (part).

Procambarus (Girardiella) hagenianus. – Hobbs, 1972b:47 (part), 151 (part), 154 (part) (by implication).

Procambarus (Girardiella) sp. D. – Fitzpatrick, 1975:385, 386, 387, 388.

Diagnosis. – Body pigmented, eyes small but well-developed. Rostrum with subparallel to gently converging margins, lacking marginal spines; acumen short, indistinctly delimited basally. Areola 38.36-41.72 (avg. 39.69)% of entire length of carapace; areola linear. Carapace devoid of cervical spines or tubercles. Suborbital angle lacking. Postorbital ridges lacking spines or tubercles cephalically. Antennal scale 2.21-3.08 (avg. 2.62) times longer than wide, widest distal to midlength, thickened lateral portion terminating in strong, acute spine. Mesial margin of palm provided with dense setiferous beard, tubercles obscure; movable finger with relatively dense tuft of setae in basal third, tuft obscuring three or four small tubercles. Opposable margin of immovable finger with row of one large and one small tubercle in basal third and third tubercle at base of distal third, distal third with crowded minute denticles; opposable margin of movable finger with row of two small, one large and one small tubercle in basal half, small tubercle at base of distal third with crowded minute denticles distal to it. Ischia of third pereiopods only with stout spine; no prominences or bosses on coxae of third through fifth pereiopods. Mesial ramus of uropod with two conspicuous spines protruding beyond distal margin. First pleopods asymmetrical, shoulder weak at base of central projection; pleopods reaching midlength of coxae of third pereiopods when abdomen flexed; distal extremity bearing (1) prominent, subacute mesial process directed distally and slightly mesially, curved caudally in distal half, extending beyond other terminal elements; (2) well-developed central projection with apical portion directed laterodistally; and (3) prominent subrhombiform (in lateral aspect) caudal process extending distally not quite so far as central projection, distal margin sloped gently caudad and caudodistal margin lamelliform. Annulus ventralis of female deeply excavate centrocephalically with strong cephalolateral ridges terminating (ventrally) without tubercles; sinus originating slightly cephalic to center of annulus, arcing gently to be lost in caudal 10% of annulus; postannular sternite broadly conical in shape.

Holotypic male, Form I. – Body subovate, distinctly compressed. Abdomen narrower than thorax (9.3 and 14.1 mm). Width of carapace at caudodorsal margin of cervical groove less than height (14.1, 14.5 mm). Areola 38.46% of total length of carapace and linear; cephalic section of carapace 1.6 times as long as areola (Fig. 95). Rostrum sharply depressed (Fig. 101), deeply excavate dorsally, with thickened lateral margins slightly converging cephalically, marginal spines
basally; upper surface sparsely punctate, usual submarginal row of setiferous punctations present. Subrostral ridges moderately well-developed to level of antennae and visible to approximate distal third of rostrum in dorsal aspect. Suborbital angle lacking. Branchiostegal spine much reduced. Carapace sparsely punctate dorsally and laterally; granulate cephalolaterally with granulations best developed just posterior to orbit and antennal scale. Cervical spines or tubercles absent. Cephalic section of telson with two spines in each caudolateral corner

(Fig. 107). Cephalic portion of epistome (Fig. 105) subovoid in outline, about as broad as long, with small cephalomedian tubercle. Antennules of usual form with well-developed spine on ventral surface of basal segment slightly distal to midlength. Antennae broken, but apparently reaching to about caudal margin of carapace; antennal scale (Fig. 106) 2.73 times longer than wide, widest distal to midlength; thickened lateral portion terminating cephalically in stout, acute spine approximately 24% of total length of antennal scale; cephalic half of mesial margin of lamellar portion provided with numerous tubercular eminences bearing tufts of setae.

Ischia of third maxillipeds with long, stiff, unmatted, dense setae arising from mesial and ventrolateral margins.

Right chela (Fig. 104) with palm inflated, moderately depressed; lateral margin nearly straight, not costate; entire palmar area covered with setiferous punctations; mesial margin of palm with mat of dense setae obscuring tubercles; row of six squamous tubercles medial to setiferous beard; mesial margin of movable finger with tuft of setae in proximal third partially obscuring row of three low tubercles. Opposable margin of movable finger slightly excavated on basal one-third; with row of two small, one large and one small tubercle in basal one-half; small tubercle at base of distal third with crowded minute denticles between it and tip of finger; finger with submedian longitudinal ridge above and below, both flanked by setiferous punctations. Opposable margin of immovable finger with row of one large, one small and two nearly inconspicuous tubercles in basal half; moderate sized tubercle at base of distal third directed ventromedially, crowded minute denticles between it and tip of finger; finger with submedian longitudinal ridge above and below, both flanked by setiferous punctations.

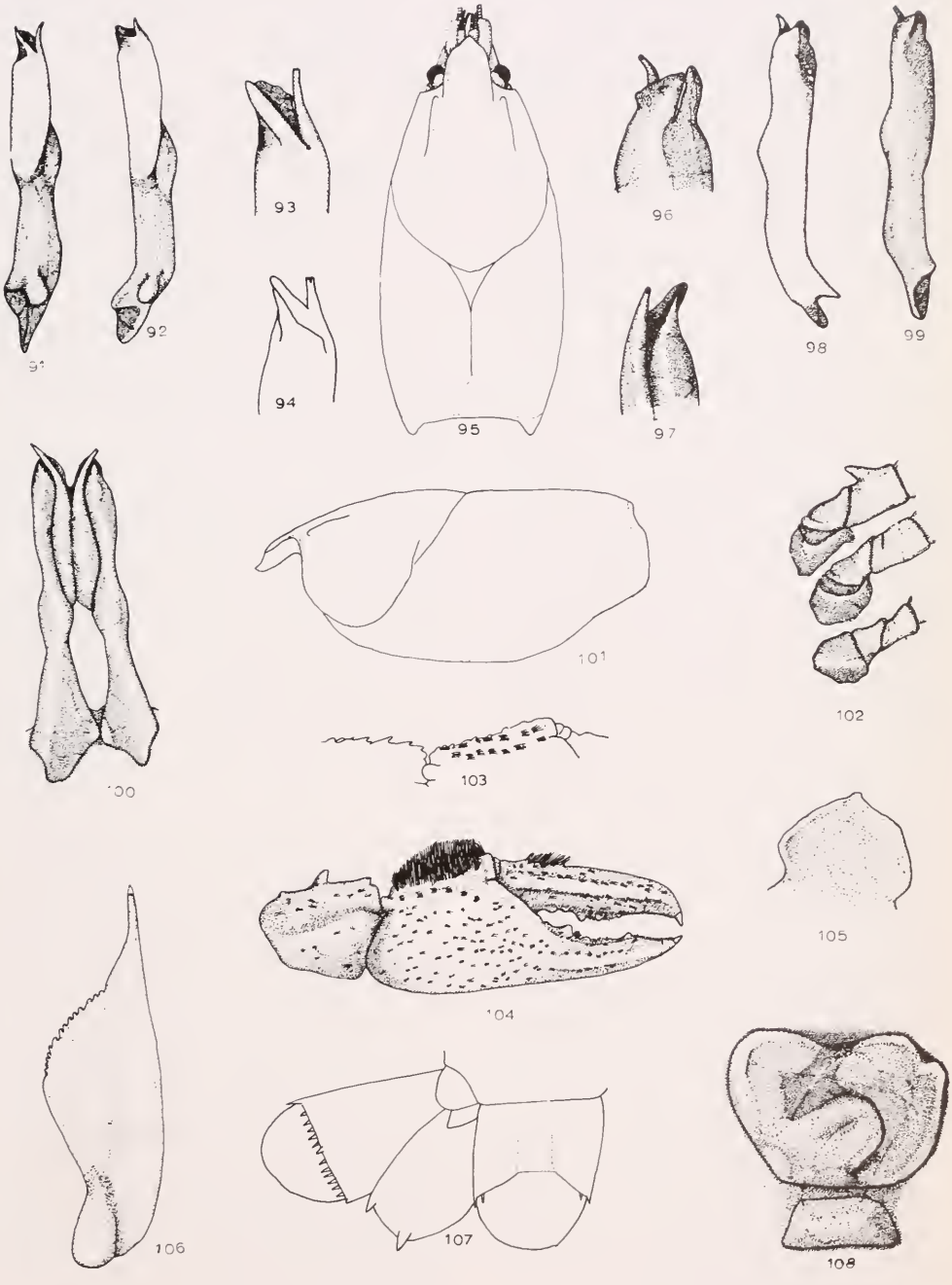
Carpus of right cheliped longer than broad with mesial margin bearing single strong acute spine slightly distal to midlength, two smaller equally spaced acute spines proximal to it, row of four squamous setiferous tubercles along middle third of mesial portion of carpus medial to aforementioned spines, small subacute spine in mesiodistal corner; punctate dorsally with longitudinal furrow slightly mesial to midline; lower distal margin with acute spines in each corner and row of three low, almost tubercular, spines between distal ventromesial corner and stout spine of mesial margin.

Merus of right cheliped with dorsal row of six tubercles terminating distally in two acute spines (distalmost strongest); ventromesial margin with row of 13 acute spines increasing in size distally; ventrolateral margin with row of seven spines, increasing in size distally. Mesial margin of ischium with row of three small but acute spines decreasing in size distally.

Hooks on ischia of third pereiopods only (Fig. 102); hooks simple and directed proximocephalically, extending just beyond distal margin of basis; coxae of third, fourth and fifth pereiopods lacking prominences or bosses.

First pleopod (Figs. 91, 93, 94, 96, 97, 99, 100) as described in *"Diagnosis"*; central projection and caudal process corneous.

Figures 91-108. *Procambarus (Girardiella) pogum* n. sp.: 91, mesial view of first pleopod of holotypic male, Form I; 92, mesial view of first pleopod of morphotypic male, Form II; 93, terminal elements of first pleopod of holotype, mesial view; 94, terminal elements of first pleopod of holotype, cephalic view; 95, dorsal view of carapace of holotype; 96, terminal elements of first pleopod of holotype, lateral view; 97, terminal elements of first pleopod of holotype, caudal view; 98, lateral view of first pleopod of morphotype; 99, lateral view of first pleopod of holotype; 100, caudal view of first pleopods of holotype; 101, lateral view of carapace of holotype; 102, proximal podomeres of third through fifth pereiopods of holotype; 103, mesial margin of palm of allotype; 104, distal podomeres of cheliped of holotype; 105, cephalic portion of epistome of holotype; 106, antennal scale of holotype; 107, telson and left uropod of holotype; 108, annulus ventralis and postannular sternite of allotype.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Uropods (Fig. 107) with mesial ramus bearing two spines projecting beyond distal margin, one from lateral corner and one, slightly larger, from median ridge.

Sternites and coxae of third through fifth pereiopodal segments bearing setae partially obscuring pleopods when latter held under thorax.

Morphotypic male, Form II. – Differing from holotype in following respects: mesial margin of palm with setiferous mat not so dense, but still obscuring margins completely; lacking tuft of setae on mesial margin of dactyl; hooks on ischia of third pereiopods not so strong, almost tubercular. Terminal elements of first pleopod (Fig. 92, 98) noncorneous, proportionately smaller and less developed; base of central projection enveloped by tightly applied fold on mesial, cephalic and lateral surfaces. Setiferous ornamentation of pereiopodal sternites and coxae less well-developed. Tip of rostrum markedly more truncate (broken early in life?).

Allotypic female. – Differing from holotype in following respects: mesial margin of palm (Fig. 103) and dactyl lacking setiferous beard, instead palm with mesial row of six tubercles and with two rows of seven each squamous setiferous tubercles median to it; row of nine spinose tubercles median to stout spine of mesial margin of carpus giving serrated appearance to upper mesial edge; spines between stout mesial spine and distal ventromesial spine of carpus strongly acute, additional row of four spines ventromesial to aforementioned spines and row of two ventromesial to stout spine of mesial margin.

Annulus ventralis (Fig. 108) deeply excavate centrocephalically, sulcus sloping precipitously cephalically; annulus set off cephalically by deep groove; quite large cephalolateral ridges lacking tubercles, extending ventrally approximately three times depth of remainder of annulus; sinus originating slightly cephalic to center of annulus and forming gentle arc sinistrally to be lost in caudal 10% of annulus; postannular sternite broadly subconical in shape.

Types. – USNM nos. 146270, 146271, and 146272 (holo-, allo-, and morphotypes, respectively); *Paratypes:* Chickasaw County, Mississippi (2 ♂♂I, 4 ♂♂II, 9♀♀). Paratypes are located at the National Museum of Natural History.

Type-locality. – Houston, Chickasaw County, Mississippi.

Range. – The species is known only from burrows at the type-locality and from 0.4 mi E of Houlka Creek where the animals were taken from burrows in a roadside ditch. The latter, the only precise locality, is associated with the Ripley formation. Apparently *P. pogum* is associated with the upper coastal plain of the Tibbie Creek drainage.

Color. – The basic color pattern of *P. pogum* is reddish, infused with henna and with lighter areas associated with the lateral carapace, the rostral margins and the postorbital ridges.

Variation. – The limits of variation as known are incorporated into the diagnosis and description sections above. Morphometric analysis was based on a total of 15 specimens (2 ♂♂I, 4 ♂♂II, 9 ♀♀). Carapace length in Form I males was 28.6-31.1, for females 26.4-37.4 (avg. 32.51) and for Form II males 24.8-34.0 (avg. 28.8). Rostrum length was 3.36-4.85 in Form I males, 4.24-5.45 (avg. 4.85) in females and 4.20-5.26 (avg. 4.59) in Form II males; width of the rostrum was 1.39-1.77, 1.17-1.51 (avg. 1.37) and 1.23-1.59 (avg. 1.41) in the same three categories, respectively. Areola length was in Form I males 2.55-2.60, in females 2.40-2.61 (avg. 2.52) and in Form II males 2.45-2.53 (avg. 2.46). Antennal scale length was 6.98-7.97 in Form I males, 7.33-9.42 (avg. 8.34) in females and 7.18-9.16 (avg. 8.37) in Form II males. Chela length was 1.48-1.51 in Form I males, 1.57-4.03 (avg. 2.01) in females and 1.67-2.03 (avg. 1.80) in Form II males; chela width in Form I males was 1.47-2.53, 0.45-2.44 (avg. 2.11) in females and 2.45-2.60 (avg. 2.53) in Form II males. Length of the mesial margin of the palm and length of the dactyl in Form I males were 2.76-3.44 and 1.58-1.68, respectively. The same two characteristics in the same sequence were in females 1.10-2.72 (avg. 2.45) and 0.76-1.72 (avg. 1.55); in Form II males

they were 2.65-2.93 (avg. 2.78) and 1.51-1.76 (avg. 1.61). Pleopod length in Form I males was 2.18-3.21 and in Form II males was 3.64-3.74 (avg. 3.68).

Specimens examined. – MISSISSIPPI: Chickasaw Co., Houston, 11 April 1936 (2 ♂♂I, 3 ♂♂II, 8 ♀♀), 0.4 mi E of Houlka Creek, no date (1 ♂II, 1 ♀).

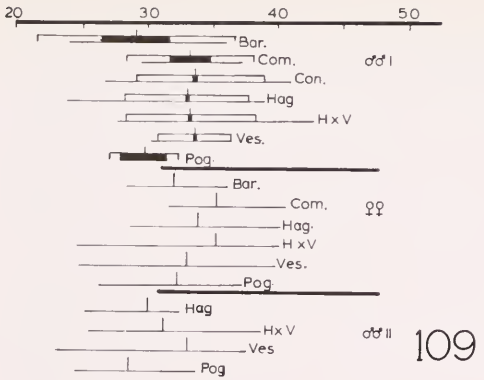
Etymology. – Taken from *pogon* (Gr.): beard; in reference to the setiferous beard found on the mesial margin of the hands in males and on the third maxilliped.

DISCUSSION

Each of the taxa described here, except *P. h. vesticeps*, probably represents a distinct breeding population of crawfish. There are many morphological features which distinguish each of the populations; likewise, there are no, again with the exception of *vesticeps*, evidences of intergradation. In each instance there seems to be either differences in ecological habitat preferences and/or physical disjunction of the habitat. Morphometric analyses strongly support the conclusions offered for other kinds of data and reveal that the several species are no more variable than other crawfish species similarly studied, exhibited no greater interspecific variation within a taxonomically compact grouping and exhibited no evidence of clines.

The most taxonomically significant differences can be found in the details of the terminal elements of the first pleopod of the Form I males. In *P. hagenianus hagenianus* and *P. h. vesticeps* the centro-cephalic process is enveloped at its base by a tight fold which becomes continuous with the centro-caudal process. A similar, but not so tightly applied, fold wraps the lateral base of the centro-cephalic process in *P. barbiger*. Contrastingly, in *P. connus* the anterior base of the cephalic portions of the centro-cephalic process has a tightly applied fold, but the fold is absent from the lateral portions. In *P. cometes* and *P. pogum* such a fold is absent. In all populations the caudal process is a broad, truncate extrusion, laterally compressed in its caudodistal half. The caudodistal margin of all, except *barbiger*, forms an angular intersection with the distal margin; in the latter this intersection is curvilinear. Only in *P. h. hagenianus*, however, is the distal margin subperpendicular to the main axis of the shaft; in all other species the margin is gently sloping, and in no species does the caudal process project distally as far as the central projection. The mesial process in all is a long, subconical, nearly setiferous protrusion extending, except in *cometes*, well beyond the distalmost portions of the other terminal elements; in *cometes* it extends distad approximately the same distance as the central projection. Only in *P. connus* is the mesial process subparallel to the main shaft of the appendage. In *P. cometes* it is curved sharply laterad, and in the remaining species it is curved gently laterad. A caudally oriented curve of the mesial process exists, additionally, in both subspecies of *hagenianus*, in *barbiger* and in *connus*, whereas in *pogum* the process curves gently cephalad to recurve gently caudad in its distal half. A pronounced shoulder occurs at the base of the cephalic margin of the central projection in both subspecies of *hagenianus*, in *barbiger* and in *connus*, although it is not sharply angular in *vesticeps* and *barbiger*. In other details the appendages are as outlined in the diagnoses above and are similar.

The most conspicuous feature of the previously undescribed taxa is the beard of plumose setae along the entire mesial margin of the palm. Such pubescence is also present in varying degrees (varying according to species) on the dactyl, on Form II males and on females, but is best developed in Form I males. All of the species bear a dense double row of plumose setae along the surface of all units of the third maxilliped. This characteristic is sufficiently common in species of primary burrowing habits to suggest an adaptation to such an habit. In *P. barbiger* and *P. pogum* the ventrolateral surface of the exopodite of the third maxilliped is provided with a dense row of heavy, stout setae forming a mat. In *P. cometes*, *P. connus* and *P. h. vesticeps* the setae of this row are stout but markedly more sparsely distributed. In *P. h. hagenianus* the row is usually absent,



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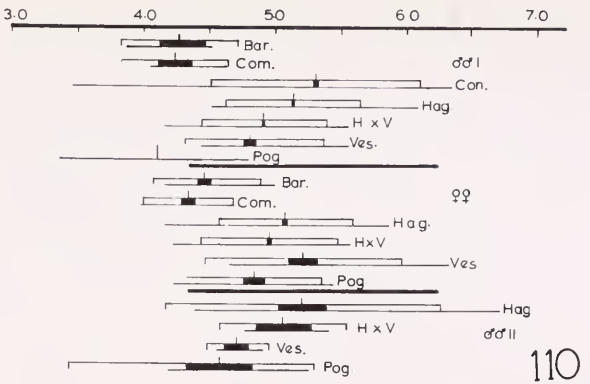

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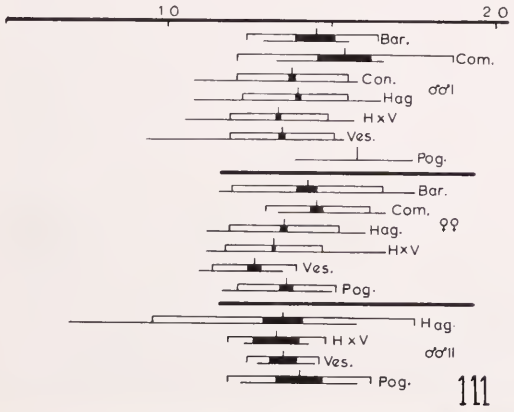

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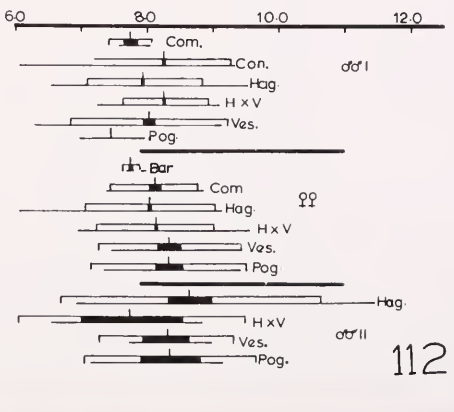

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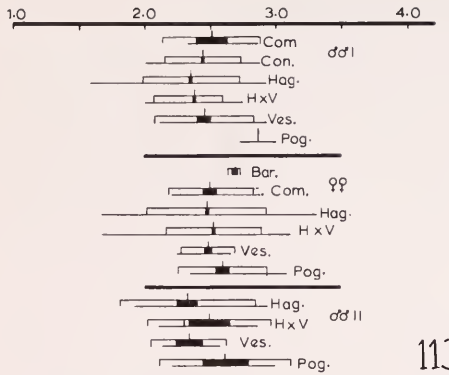
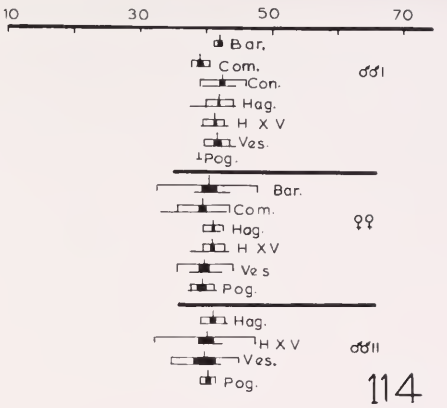
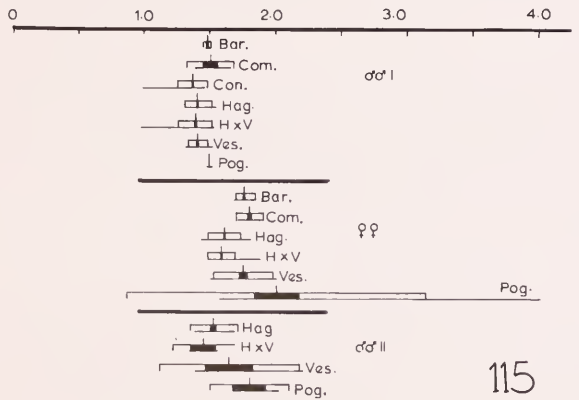
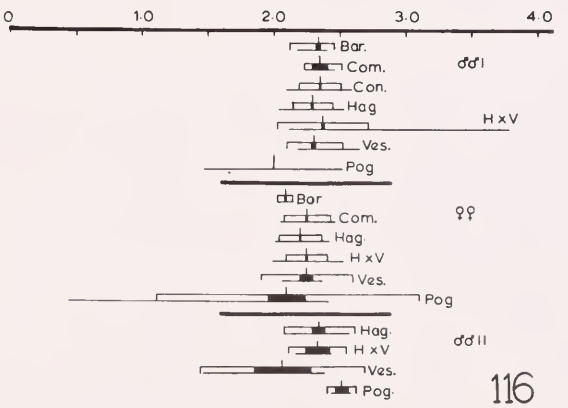
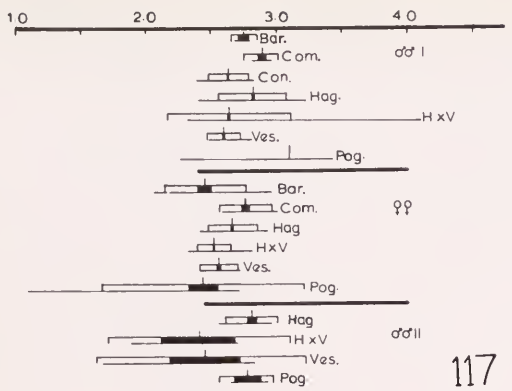








Figures 109-119. Morphometric variation in Hagenianus Group crawfishes (horizontal lines = range, vertical lines = mean, solid horizontal bars = 2 standard errors of mean, open horizontal bars = 1.5 standard deviations); species abbreviations are: Bar. = *P. (G.) barbiger,* Com. = *P. (G.) cometes,* Con. = *P. (G.) connus,* Hag. = *P. (G.) h. hagenianus,* H x V = *P. (G.) h. hagenianus* x *vesticeps,* Ves. = *P. (G.) h. vesticeps,* Pog. = *P. (G.) pogum;* ratios as described in text: 109, carapace length (in mm); 110, rostrum length; 111, rostrum width; 112, antennal scale length; 113, antennal scale width; 114, areola length (as % length of carapace); 115, chela length; 116, width of palm; 117, length of inner margin of palm; 118, dactyl length; 119, pleopod length of males.



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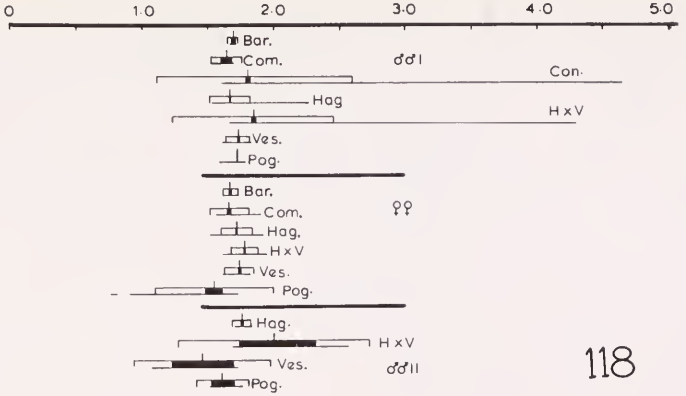

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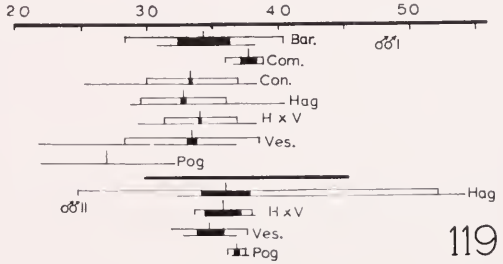

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Figures 109-119. Morphometric variation in Hagenianus Group crawfishes. Legend on Preceeding page.

but if present, at best consists of a very thin row of delicate setae.

The antennal scale reflects the degree of setation found along the hand of Form I males in every species. In *P. h. hagenianus* the setae are restricted to the short bristles common along the mesial margin in most crawfishes. In *P. barbiger* they are longer and stouter; in all of the other taxa the mesiocephalic margin is provided with tufts of long setae arising from tubercular eminences on the margins. The antennal scale is widest approximately at midlength in *P. barbiger, P. cometes, P. connus* and *P. pogum,* but it is widest distal to midlength in the subspecies of *P. hagenianus.* In all taxa the thickened lateral margin terminates distally in a strong acute spine, although the relative length of the spine varies according to the species. In *P. barbiger, P. cometes* and *P. pogum* it constitutes about 33% of the total length of the scale; in *P. connus* it is about 25% of the length; and it is about 10-15% in the subspecies of *P. hagenianus.* The spine is markedly more attenuate in the first three mentioned species than in the others and reaches the other extreme in *P. h. vesticeps* in which it is nearly conical in shape. Other variations are mentioned in previous discussions.

A much more difficult characteristic to evaluate is the annulus ventralis of the female. All have an annulus in which there is an anterior trough (sulcus) which rises caudally; the highest (ventrally) portions are cephalolateral and/or lateral, and the annulus is movable; usually the prominences are decorated with tubercular eminences. In the subspecies of *P. hagenianus* and in *P. pogum* the anterior portion of the sulcus slopes precipitously toward a deeply excavate sternum associated with the fourth pereiopodal segment. The annulus is poorly delineated from the sternum associated with its anterior margin in the subspecies of *P. hagenianus,* but in *P. pogum* is set off by an intervening groove. The annulus of *P. barbiger* has a less severe slope and is delineated anteriorly from the sternite by a groove. In *P. cometes* the anterior sulcus is narrow, less sloped and delimited anteriorly by a groove. The postannular sternite (associated with pereiopodal segment V) is subconical in *P. h. hagenianus* and *P. cometes,* broadly conical in *P. h. vesticeps* and *P. pogum,* but in *P. barbiger* is in the shape of a triangular prism.

In morphometric analysis 10 characteristics were analyzed in males and nine in females. For analysis the males were treated as two separate categories — Form I and Form II. Thus, 29 comparisons could be made between any two populations. When these comparisons were made using a null hypothesis, the following significant ($p \geq 0.05$) differences were established (Table 1): *P. h. hagenianus* differed from *P. h. vesticeps* in 24 characteristics, from *P. barbiger* in 14 (of 19), from *P. connus* in 5 (of 10), from *P. pogum* in 21 and from *P. cometes* in 14 (of 19). *P. h. vesticeps* differed from *barbiger* in 10 (of 19), from *connus* in 8 (of 10), from *pogum* in 21 and from *cometes* in 18 (of 19). *P. barbiger* differed from *connus* in 4 (of 19), from *pogum* in 7 (of 10) and from *cometes* in 6 (of 19). *P. connus* differed from *pogum* in 6 (of 10) and from *cometes* in 7 (of 10); and *P. pogum* differed from *P. cometes* in 12 (of 19). In many of these $p \geq 0.01$. The report of less than all possible combinations results from the fact that no Form II males are known for *P. barbiger,* and there are insufficient numbers for analysis in the category of Form II males for *P. cometes* and *P. connus* and for females in *P. connus.*

Procambarus barbiger and *P. connus* seem to be geographically isolated from the other species, and the latter is the only one associated with loess. The subspecies of *P. hagenianus* are apparently restricted to the prairie soils of the Black Belt of Alabama and Mississippi, with the nominate subspecies occupying the area south and east of Tibbie Creek, a tributary to the west bank of the Tombigbee River in east-central Mississippi; an intergrade population occurring just north of the creek; and *P. h. vesticeps* being confined to the upper Tombigbee River system (Fig. 120). *P. cometes* and *P. pogum* occupy limited areas in different habitats just outside the periphery of the range of *P. hagenianus;* both are associated with the interior flatwoods.

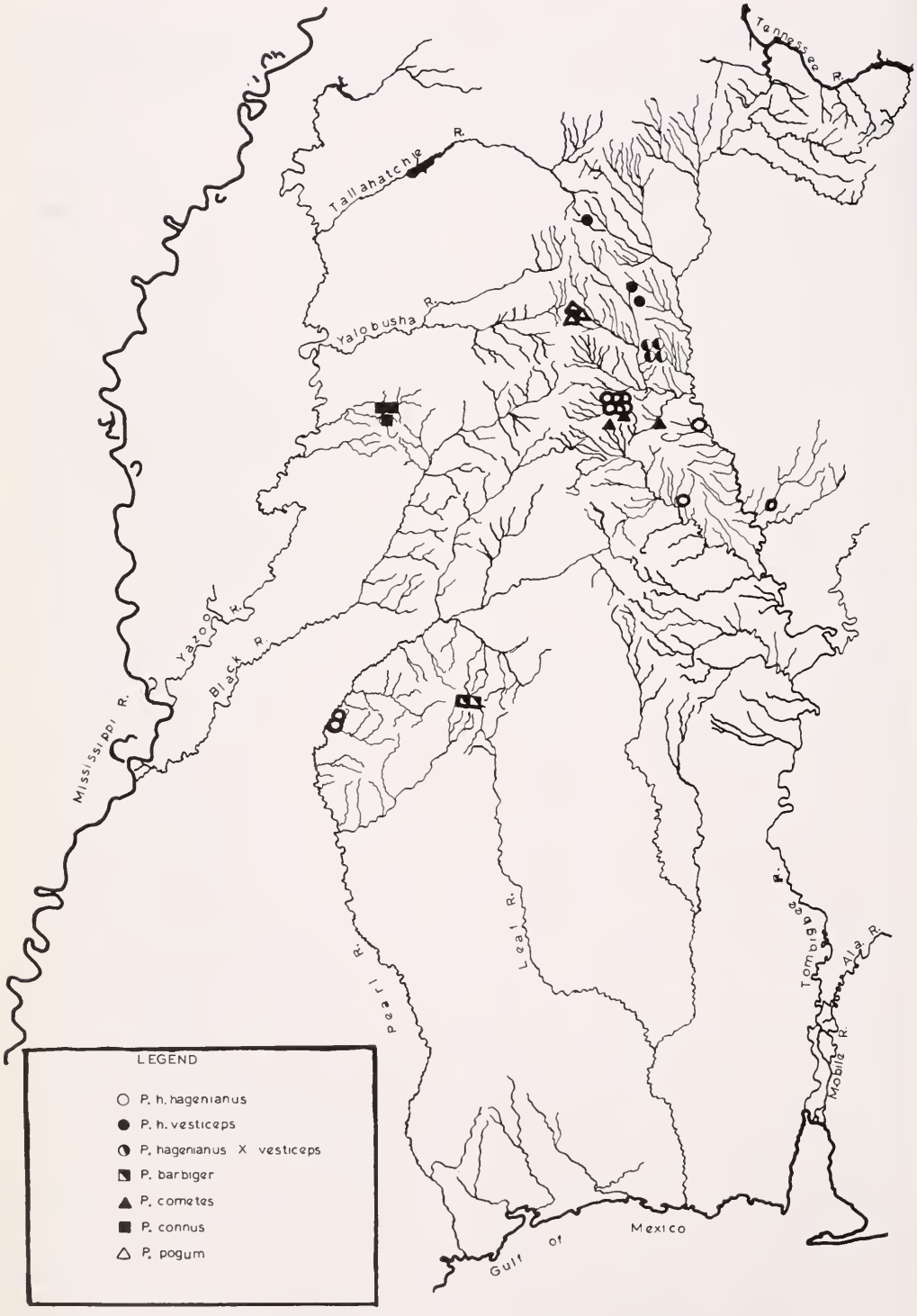

Figure 120. Distribution of Hagenianus Group crawfishes.

The species of the Hagenianus Group probably represent a derivative stock rather than an ancestral stock within the subgenus *Girardiella*. The loss of the cephalic process, present in all other species of the subgenus, is an excellent indication that this group is unlike the ancestral stock. Four taxa—*h. hagenianus, h. vesticeps, barbiger* and *connus*—possess a highly specialized structure in the fold which envelops the base of the central projection. All Hagenianus Group species have a nearly unique spinose ornamentation on the uropods, indicating a secondarily acquired characteristic. In the subgenus, the most generalized pleopod is probably found in *Procambarus (Girardiella) gracilis*, but the relatively broad areola found in *P. (G.) tulanei* is generally considered to be a more primitive condition in crawfishes than the obliterated or linear areolae characteristic of species of the subgenus. Bearding of the hands and maxillipeds is a more widespread phenomenon, but general consensus favors the unbearded hand as the more primitive condition in crawfishes. *P. tulanei* becomes interesting in a study of the Hagenianus Group because it seems to fill certain essential criteria as a form intermediate between the two species complexes constituting the Gracilis and Hagenianus Groups. Geographically, it is found in the Red and Ouachita River systems of Arkansas and Louisiana; the other taxa of the Gracilis Group are found in an arc and are northeast to southwest of it. It is the only member of this assemblage with a beard of long setae along the mesial margin of the palm, while *P. h. hagenianus* is the only member of the Hagenianus Group to lack it. The broad areola has already been mentioned. Thus, as I have previously outlined (Fitzpatrick, 1975), a *tulanei*-like stock is not an unreasonable candidate for the ancestral population, the Gracilis Group constituting modern descendants most like the ancestor.

The routes by which the Hagenianus Group populations came to occupy the present habitats are difficult to assess. Two possible avenues of invasion exist. They may have come by a southerly route, or they may have come from the northwest, crossing the Mississippi River in the vicinity of Memphis or likely more northward. The former route, with a crossing associated with the Vicksburg-Natchez area, is unlikely. To perform a southerly crossing they would have had to cross a relatively wide band of loess, a type of material not well suited to primary burrowing crawfishes. Another problem to their dispersal is the intervening flood plain of the river. Everywhere south of the confluence with the Ohio River this flood plain is quite wide, but south of Memphis, excepting the Natchez area, it becomes even wider to develop into the extensive Delta Plain of southern Louisiana. Fitzpatrick and Hobbs III (1968) have argued that the Mississippi River acts as a zoogeographical barrier to the dispersal of certain species of crawfishes and probably other aquatics principally by the interposition of the flood plain as an ecological barrier. Thus, direct connection between the *tulanei* population progenitors and the Hagenianus Group ancestors in an east-west pattern is quite unlikely.

On the other hand, the species complex currently identified as *gracilis* occurs, in part, east of the river north of the Ohio River confluence. Broad bands of Tertiary and Cretaceous deposits can be found in western Tennessee and Kentucky. A more likely avenue for invasion, then, may be associated with these features. Thus, the prairie substrate can be seen as exploitation of an available habitat rather than a center from which expansion occurred. The habitat of *P. connus* is probably not the source from which radiation occurred. The loess and/or sandy substrates around Carrollton are not suited to a primary burrower. Several morphological features of *P. cometes* suggest that it does not represent the ancestral population. The mesial process of the first pleopod of the Form I male is subequal to the central projection, a condition unique in the subgenus. The sulcus of the annulis vertralis is markedly more narrow than in any of the related species, and the first pleopod lacks a shoulder on the cephalic surface near the base of the central projection.

As noted, the subspecies of *P. hagenianus* have many specializations which indicate

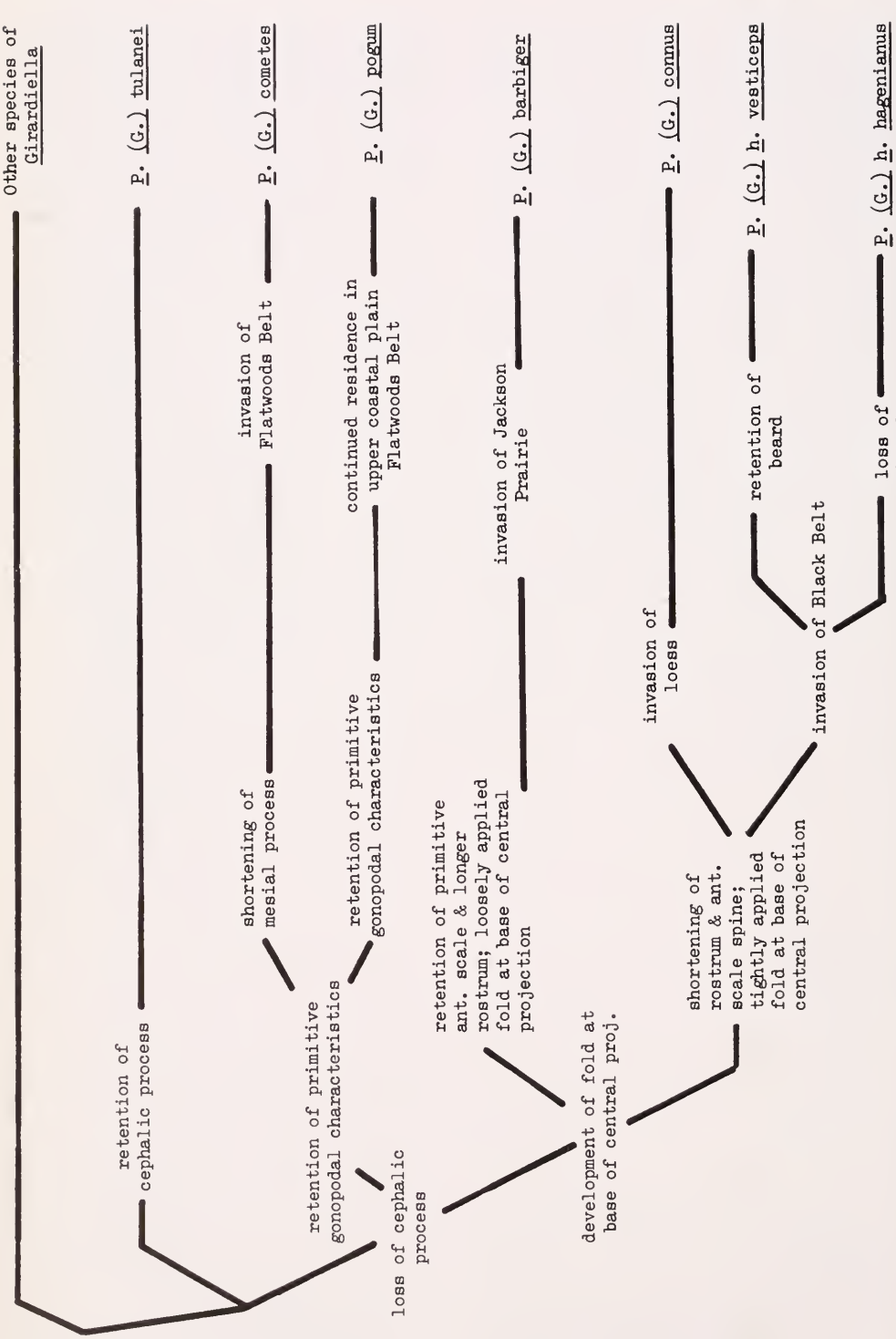
Other species of Girardiella
P. (G.) tulanei
P. (G.) cometes
P. (G.) pogum
P. (G.) barbiger
P. (G.) connus
P. (G.) h. vesticeps
P. (G.) h. hagenianus
retention of cephalic process
retention of primitive gonopodal characteristics
loss of cephalic process
shortening of mesial process
invasion of Flatwoods Belt
retention of primitive gonopodal characteristics
continued residence in upper coastal plain Flatwoods Belt
retention of primitive ant. scale & longer rostrum; loosely applied fold at base of central projection
invasion of Jackson Prairie
development of fold at base of central proj.
shortening of rostrum & ant. scale spine; tightly applied fold at base of central projection
invasion of loess
retention of beard
invasion of Black Belt
loss of beard

Figure 121. Proposed relationships of Hagenianus Group crawfishes.

that they do not represent the population from which the Hagenianus Group stock descended, and their prairie soil habitat does not represent a continuum through which invasion could take place. Although *P. barbiger* seems to retain several features which associate it with the primitive stock (bearded hand, lamellar portion of antennal scale lacking a tubercular margin, and a groove at the anterior margin of the annulus), it also has some unique and probably derived characteristics: the beard of the hand occurs in distinct tufts; the distal margin of the caudal process has a curvilinear relationship with the caudal margin rather than angular; the lateral base of the central projection is covered by a loosely applied fold; and the postannular sternite is uniquely in the shape of a triangular prism. Couple these morphological features with the prairie-habitat difficulty mentioned above, and one is inevitably drawn to the conclusion that this species represents a secondary, albeit early, invasion of an available habitat.

Thus, one is left with one species, *P. pogum*, having relatively primitive characteristics within the group and occupying a habitat compatible with an environmentally plausible invasion route. But *pogum* does not in itself represent a relict of the ancestral stock. Several features indicate that it, too, has undergone specialization. The shoulder at the base of the central projection is lacking in *pogum* and only one other species in the subgenus, *cometes*. Only in *pogum* in the Hagenianus Group is the mesial process recurved distally, and the slope of the sulcus of the annulus ventralis falling precipitously toward the anterior margin is more like the derivative *hagenianus* populations than the other species. The antennal scale is an excellent structure to indicate the mixed combination of characters found in this species: primitive features include a long spine forming the distalmost part of the thickened lateral portion (33% as in *barbiger* and *cometes*, compared with 25% in *connus* and 10-15% in the subspecies of *hagenianus*) and being widest near midlength (as in *barbiger*, *cometes* and *connus*). On the other hand, it shares the apparently derived condition of having setae arising in tufts from tubercular prominences along the cephalic portion of the lamellar margin with *cometes*, *connus* and *h. vesticeps*.

The picture presented, then, is one in which a crawfish stock entered the area across the Mississippi Flood Plain from the northwest probably in a single invasion. But shortly after invasion an adaptive radiation occurred resulting in the reproductive isolation of five populations, with the easternmost filling the most expansive habitat and undergoing clinal (?) variation which eventually resulted in geographic races. Suggested relationships are given in Figure 121.

A Key to the Hagenianus Group of Crawfishes

In Hobbs' (1972b:45) "Key to Species of Subgenus *Girardiella*," couplet 1 must be modified as follows (*italics* indicate changes):

1 Mesial surface of palm of chela bearded; areola *always* with 3 or 4 punctations across narrowest part; *cephalic process present* . . . . . *P. (G.) tulanei* Penn.

Mesial surface of palm of chela never bearded, *or if bearded areola linear and cephalic process absent*, areola linear or with only 1 or 2 punctations across narrowest part. . . . . 2.

The keys here offered may then be used following identification of *P. hagenianus* in couplet 4. Alternately, after eliminating the genus *Fallicambarus* and the subgenus *Acucauda* from consideration, one may proceed directly to this key if the specimens possess a median spine extending beyond the distal margin of the inner ramus of the uropod.

1	Sex male	2.
1'	Sex female	7.
2 (1)	Mesial margin of palm with setiferous beard.	3.
2'	Mesial margin of palm lacking setiferous beard. . . . . *P. h. hagenianus* (Faxon).	
3 (2)	One or more tufts of long setae arising along mesial margin in basal half of dactyl.	4.
3'	Dactyl lacking tufts of long setae along mesial margin.	5.

4 (3) Tufts of setae on dactyl scanty; tight fold enveloping base of central projection in Form I male. . . . . *P. connus* n. sp.

4' Tufts of setae on dactyl well-developed; base of central projection of Form I male lacking enveloping fold. . . . . .*P. pogum* n. sp.

5 (3') Mesial process of first pleopod subequal to central projection in length; lacking enveloping fold at base of central projection in Form I males. . . . . .*P. cometes* n. sp.

5' Mesial process of first pleopod longer than central projection; base of central projection enveloped by fold in Form I males. . . . . 6.

6 (5') Distal margin of caudal process of first pleopod subperpendicular to main axis of shaft of pleopod; setae of lamellar portion of antennal scale arising in tufts from tubercular eminences. . *P. h. vesticeps* n. subsp.

6' Distal margin of caudal process of first pleopod not subperpendicular to main axis of shaft of pleopod; setae of lamellar portion of antennal scale arising individually. . . . .

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ECOLOGY AND POPULATION DYNAMICS OF THE BLACK BULLHEAD, *ICTALURUS MELAS* (RAFINESQUE), IN CENTRAL KENTUCKY

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ABSTRACT

The black bullhead, *Ictalurus melas* (Rafinesque), is a prominent element of the fish fauna in central Kentucky, but relatively little has been reported concerning either the population dynamics or physiological ecology in that area. This work reports growth and reproduction in pond, lake and stream populations of the black bullhead. Emphasis was placed on pond populations for the analysis of reproductive development, longevity and survival. Some aspects of the physiological ecology, including temperature ranges and oxygen consumption rates, were measured as functions of prior acclimation histories.

Black bullheads were well-represented in each of the habitats surveyed; however, growth in length and in weight, expressed as a function of age at the time of annulus formation, was significantly lower for fish taken from ponds. Pond populations exhibited the ability to achieve great numbers, and the effect of crowding was significantly reflected in lower length-weight and age-weight correlations, and in lower mean fecundity. Mortality in ponds was high throughout the year, and highest during spring and early summer. Adult black bullheads sampled from all populations relied heavily on chironomid larvae as a staple source of food, although this item had a selection value comparable to several less abundant food sources. Larval feeding was found to be highly selective. Reproductive development, and the attainment of peak gonad weight-body weight ratios was retarded in ponds as compared with development in lakes and streams. Temperature thresholds measured at 7°, 12° and 23°C indicated that different life stages responded differently to temperature. Upper critical thresholds for the first four free-swimming stages formed a graded sequence, with lower thresholds graduated upward in direct proportion to upper critical values. Preference ranges differed significantly for postlarval through yearling stages. Oxygen consumption rates, Q10 values, and absolute consumption curves suggested a relative insensitivity to temperature. Black bullheads ranging in weight from 20.15 to 37.00 g had a critical oxygen consumption value per gram of 0.1 ml. O_2/g/hr at 0.2 to 0.5 ml/l ambient oxygen.

INTRODUCTION

Changes in fish stocking combinations (Swingle, 1950), shifts in angler preferences (Houser and Collins, 1962) and selective construction of commercial gear to favor larger, if less abundant, fishes have deemphasized the value of the black bullhead. Although management personnel and anglers in Kansas and Iowa (Hastings and Cross, 1962; Forney, 1955) continue to prize this species for its angling value most states east of the Mississippi River have shown little interest in bullhead propagation and management for sport or commercial purposes since early in the present century.

General disregard for the black bullhead is reflected in the early complete absence of investigations designed to foster a better understanding of its potentials and limitations. In short, very little is known concerning many important aspects of the life history and physiological ecology of *I. melas*, aspects that might prove valuable if the species is to be most effectively utilized or managed. No detailed bullhead investigations have been conducted in Kentucky waters. Reports that have appeared (Clay, 1962) have simply acknowledged the

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species' presence and recorded some of its taxonomic features.

The purpose of this study is to present pertinent aspects of the black bullhead life cycle in order to assess the species' ecological interactions, and to analyze some physiological phenomena which favor the fish in some habitats and restrict it in others. The study was begun in April 1970 and terminated in early July 1971. During this period, our investigation concentrated on the reproductive potential, natural mortality, feeding behavior and food, and physiological ecology associated with the black bullhead's success in natural and impounded waters, with particular emphasis on the earlier stages of life. However, several aspects of adult biology not previously investigated in Kentucky waters were studied with significant results.

REVIEW OF THE LITERATURE

Black bullheads have been found in virtually every type of fresh-water habitat. Houser and Collins (1962), for example, indicated that no important Oklahoma water was free of this species. Although sampled from reservoirs, lakes and streams, the only significant populations were encountered in smaller bodies of water. This finding is supported by the results of lake and stream investigations conducted throughout the range (Lynch, Buscemi and Lemmons, 1951; Trautman, 1957). According to Fogel (1964), black bullheads comprise an insignificant 0.5 to 1.5 per cent of the annual catch in South Dakota waters, and Clark (1960) listed the black and brown bullheads as the least important species encountered in Lake St. Marys, Ohio, as reflected by annual harvest statistics. He added, however, that strong year classes occasionally appear, which assure well-balanced distribution of the species.

Important populations of bullheads and channel catfish *(I. punctatus)* formerly occurred in the Mississippi River and its tributaries. According to Barnickol and Starrett (1951), this species complex amounted to 50% of the commercial catch reported in 1899. This figure had dwindled to 15.1 per cent by 1946 corresponding to concommitant increases in the populations of other commercial species, particularly carp and buffalofishes (Barnickol and Starrett, loc. cit.).

Black bullheads have become prominent in small artificial lakes in many areas of the midwest (Jenkins, 1959), sometimes to such an extent that selective eradication projects have been directed toward population reduction (Houser and Grinstead, 1961). The greatest predominance appears to be in farm ponds where the management objective may or may not be bullhead propagation (Bennett, 1952). In Douglas County, Kansas, Hastings and Cross (1962) found black bullheads in 15 of the 22 farm ponds surveyed (68 per cent), and considered them as dominants in 14 of these.The ponds studied were aribtrarily classified on the basis of turbidity: 50 ppm or less suspended material constituted a clear pond, while one exceeding this limit was considered turbid. Black bullheads predominated in all turbid ponds for which quantitative estimates were obtained. Trautman (1957) found that black bullheads have increased in Ohio waters during the present century at the expense of other bullhead species. Increased siltation resulting from more intensively applied agricultural practices apparently has favored this replacement trend.

Differences in ponderal indices from different portions of Clear Lake, Iowa, suggested that several subpopulations could exist in the same body of water (Forney, 1955). Each of these subpopulations exhibited its own vital characteristics based, in part, on differences in food supplies. Various authors have attributed the distributional success of black bullheads to omnivorous feeding habits (Clay, 1962; Viosca; 1931; Smith, 1949), although Forney (1955) indicated that selective feeding occurred in Iowa. Rose and Moen (1951) concluded that selective feeding by adults was more apparent than real, usually reflecting the preponderance of one or more items over others in the food supply. Kutkuhn (1955) listed a variety of food items taken by adult black bullheads in Iowa lakes: insects, ento-

Foods taken by different age groups appear to differ significantly, resulting in part from differences in feeding times between adults and young. Darnell and Meierotto (1965) found that young-of-the-year bullheads school during the day, their social appetites stimulated by tactile and gustatory senses not shared by older individuals (Bowen, 1931). Adults were rarely active by day but commenced feeding with the onset of darkness and remained active throughout the night. Young bullheads (15 - 53 mm TL) in Clear Lake, Iowa, fed almost exclusively on Entomostraca (Forney, 1955). Ewers (1931) found that small bullheads (36 - 76 mm TL) in Buckeye Lake, Ohio, fed primarily on the amphipod *Hyalella*, Entomostraca and small insect larva, with peaks of feeding activity occurring just before dawn.

Feeding preferences appear to change sequentially with different stages of the reproductive cycle. Raney and Webster (1940), working with Cayuga Lake bullheads in New York, noted the following feeding pattern: adults moved into cover during periods of 50° to 55°F temperature (early April) and began feeding avidly on aquatic vegetation *(Nymphozanthus advena* and *Potamogeton)* prior to spawning. Throughout the remainder of the year, feeding habits were assessed as truly omnivorous. Forney (1955) noted a similar sequence, and concluded that plant feeding was somehow related to the attainment of reproductive readiness. He listed as staples throughout the first year of life, Crustacea (60 per cent) and Diptera larva (25 per cent, chiefly Chrionomidae). The inclusion of adult dipterans and bryozoan statoblasts suggested some surface feeding data, but such activity has not been described.

Age and growth statistics, vital to an understanding of any species' population complexities, have been reported from various states (Carlander, 1968); however, none have appeared representing the bullheads of Kentucky waters. Synthesis of the available material yields the following generalizations: growth tends to be more rapid in clear water, notwithstanding the black bullhead's propensity to dominate turbid waters (Hastings and Cross, 1962). Bullheads in Kansas and Iowa ponds tended to overcrowd turbid waters, rarely maintaining suitable growth rates. Houser and Collins (1962) noted slower growth rates in steeams than in ponds or reservoirs. Variations in growth rates have been so extreme throughout the range that comparisons for different habitat types are all but precluded (Carlander, 1968), as in the case of direct comparisons of Kentucky populations with others.

Albaugh (1969) found great intraspecific variability in growth per season. In artificial ponds provided with unlimited food supplies, males made greater gains than females, but when food supplies were kept near maintenance levels, growth rates were comparable. Simco and Cross (1966) reached similar conclusions concerning differential growth rates in *I. punctatus.*

Growth is apparently rapid during the first year of life, and subsequently slower coincident with the degree of intraspecific competition. Moen (1959) noted that bullheads in Silver Lake, Iowa, attained an average total length of 127 mm in September at age I, but only 132 mm (41 g) in September at age II. Following a severe winter kill, which significantly reduced competition, these same fish reached a length of 201 mm and 122 g at age III. The age IV group increased from 208 mm to only 213 mm at age V. Corthell (1961) assessed rapid growth of bullheads in the Empire Lakes, Oregon, as the result of recent introduction and low population density.

Some of the most worthwhile data pertinent to the management of scaled fish has been gained through the evaluation of age-growth relationships based on the scale method of age determination (Creaser, 1926; Buckman, 1929, Van Oosten, 1929). Since members of the genus *Ictalurus* lack scales, workers have resorted to annuli on bones and spines for age determination (Lewis, 1949, 1950; Forney, 1955; Carlander and Sprugel, 1948; Sneed, 1951). Houser and Collins (1962) found that annuli usually

formed on fin spines during the second week in May in Oklahoma waters. The uniform appearance of annuli from all age groups at the time indicated that all ages developed annuli at approximately the same time.

Few descriptions of the breeding behavior of *I. melas* are available. The early ichthyological notes of Fowler (1917) provided the following account. (It should be noted, however, that the author referred to the breeding pair simply as "bullheads", leaving some doubt as to their species identity.) "After a nest was constructed by the female, both sexes took charge of it; both guarded the eggs and the fry after spawning; and both were observed occupying the nest at the same and at alternate times. The deposited eggs numbered 200, were creamy white in color, and took approximately five days to hatch." Wallace (1957), in a more recent account, found that only the female excavated the nest. As the nest neared completion, each parent began to pay closer attention to the other. Actual spawning lasted for about one second, and occurred five times in a single hour. The female guarded the eggs during the first day, the male thereafter. Clemens and Sneed (1957) described a similar behavior in the channel catfish.

Black bullheads reportedly make no elaborate preparation for spawning, although gonadal development comprises a relatively long period of time. Dennison (1970) found reproductively mature males and females during the 1969 season in Clear Lake, Iowa, starting to mobilize material in the gonads for the next spawning season during August and September. Mesenteric fat was assumed to be the principal source of energy for gonadal development. Differences in the availability of mesenteric fat between the 1969 and 1970 seasons were reflected in the success of spawning and in fecundity indices.

Because of wide variation in weight at a given length within the rather narrow length range for mature bullheads, the value of the length-weight relationship as a measure of reproductivity is considerably reduced. Nevertheless, length has been used as an arbitrary index to reproductive readiness. Mississippi River bullheads with a total length of 154 mm or more, and belonging to age group III were considered reproductively mature by Barnikol and Starrett (1951). A similar range was proposed by Shields (1957a, b) for the bullheads of Gavins Point Reservoir, South Dakota. Dennison (1970) arbitrarily chose 229 mm total length as the size separating mature and immature bullheads in Clear Lake, Iowa.

Fecundity appears to be more closely related to length than to age. Clear Lake females, for example, 203 to 226 mm in total length contained and average of 3,283 eggs, while females of the same population 229 to 251 mm long contained an average of 3,845 eggs (Forney, 1955). Dennison (1970) noted a good relationship between length and fecundity in bullheads. Adult females with an average length of 250 to 259 mm had a mean fecundity of 3,892 eggs. Limits of fecundity throughout the range could not be determined, since few statistics, other than those listed above, are available (Carlander, 1968).

Few attempts have been made to establish the periods of reproduction for black bullheads. Chance observations of spawning periods have been the rule rather than the exception. Spawning occurs from late June to late July in South Dakota (Shields, 1957a, b). The earliest spent female was taken on June 26, and the latest ripe female on August 6, 1951 in Clear Lake (Forney, 1955). Dennison (1970) reported that the 1969 spawning season in Iowa extended from June 1 through July 1, while the 1970 season was somewhat shorter (June 10 to 23), each seasonal limit reflecting the influence of prolonged temperature increase.

The literature is incomplete with respect to environmental conditions that influence initiation of the spawning response. Buser and Blanc (1949) tested the effect of photoperiod on gonadal development in *I. nebulosus*. Continuous light in winter produced increase in testicular and ovarian weight, accompanied by increased in the deposition of interstitial tissue. According to Burger (1939) and Medlen (1951) temperature was a more influential factor than light for a number of fishes (see also, Liley, 1969; Har,

1965). Wallace (1967) observed spawning in captive bullheads that had been retained in the laboratory from August through March. Environmental conditioning was not intended, i.e., photoperiod control was not maintained, and temperature was held at a constant 25°C. The absence of control did not inhibit induced spawning. Dennison (1970) stated that spawning was triggered by an abrupt increase in water temperature, ranging from 6° to 8°C over a period of several days.

Any fish that lives in farm ponds is subjected to seasonal and sudden changes in temperature, but not necessarily in light intensity (Wallen, 1955). The Secchi disk visibility in Oklahoma ponds, determined on 132 occasions from 1951 to 1954 averaged only 45.7 cm. Readings of 6 mm, varying slightly throughout the year, were recorded for some turbid waters known to contain bullheads.

Accounts of black bullhead embryonic development are scarce. Spawning seems difficult to induce in the laboratory, since even reproductively mature individuals often become refractory under imposed conditions (Sneed and Clemens, 1960). To avoid this difficulty, especially where regulation of spawning is economically important, several methods have been devised to heighten or induce spawning. The dependence of sexual behavior on the gonadal secretions of fish is well-authenticated (Jones and King, 1952; Cohen, 1946; M.C. Tavolga, 1949). There is, however, experimental evidence to indicate that sexual behavior and spawning attempts may be influenced by pituitary hormones in the absence of gonadal mediation (Noble and Kumpf, 1936). Hypophysectomy, on the other hand, can cause the complete cessation of the behavioral sequence which normally leads to spawning (W.N. Tavolga, 1955).

An authoritative review of the role of pituitary hormones in spawning, and the use of excised pituitary glands in pisciculture has been presented by Pickford and Atz (1957), and specific accounts have appeared periodically (Robinson and Rinfret, 1957; Schmidt, et al. 1965; Graybill and Horton, 1969). Sneed and Clemens (1957) dealt with induced catfish spawning, a method used successfully to influence the sequence of bullhead reproduction by Wallace (1967).

Several investigators have commented on the ability of black bullheads to survive in waters that are uninhabitable for most other species (Black, 1953, 1955; Lewis, 1949; Trautman, 1957; Bennett, 1948). Bullheads have apparently evolved certain adaptive mechanisms which elevate tolerance levels in contrast to less hardy species. Hathaway (1927) found little change in feeding and behavior patterns with markedly increased water temperatures, and Bailey (1955) described the chance observation of mass-mortality in Bass Lake, Michigan. Death to a complex of species was assessed as the result of high temperature, since none of the characteristic signs of anoxia were apparent. Ictalurid fishes were the least affected; a water temperature of 38°C was not limiting to the catfishes so long as free movement was assured.

Temperature relation analyses of poikilothermic animals are extensive in the literature (Bullock, 1955; Precht, et al. 1955). Brett (1956) measured the median resistance times of several species of fish that were tested at various high temperatures and acclimated at 20°C. The upper incipient lethal temperature (the point at which no further death occurred with time) for *I. nebulosus* fell between 32°C and 33°C. Morris (1965) reported similar information for the yellow bullhead, a species he found adaptable to extremes of both heat and cold. Black (1953) found that black bullheads acclimated at 23°C had an upper lethal temperature of 35°C, but she failed to report the effects of cold and associated lethal temperatures.

Cowles and Bogert (1944) introduced the concept of critical thermal maximum (CTMax). According to these authors, upper lethal temperatures have little ecological significance, since species in nature will usually be prevented from reaching extremes. The critical thermal maximum was subsequently defined as the thermal point at which locomotory activity becomes dis-

organized, and the animal loses the ability to escape conditions that would promptly lead to its death. According to this definition, physiological and ecological death points do not necessarily coincide, and may, in fact, be widely separated. A similar argument could be posed for critical thermal minimum (CTMin).

The ecological significance of temperature thresholds in fish has been questioned by Hart (1952) and Brett (1959), who contended that temperature tolerances are usually well above habitat extremes. Critical thermal determinations that reflect the ecological rather than physiological death range have also been considered more valid than incipient lethal temperatures by Lowe and Heath (1969). Few CTM determinations have been made for freshwater fish, presumably because of the difficulty associated with determination of the ecological death point (Hutchison, 1961; Norris, 1963).

Forbes and Richardson (1909) stated that bullheads cease feeding and become sluggish, sometimes burrowing into the mud, in late fall. Underhill (1952) demonstrated that, although brown bullheads acclimated to 10°C showed reduced rates of feeding, they did continue to feed throughout the year, and Nordlie (1966) noted that black bullheads, which remained relatively active throughout the winter, had peptic digestive rates that could be correlated to acclimation histories. The extent to which other physiological functions depend on temperature, and the limits to which these dependences can be expected to adjust, have been poorly authenticated for ictalurid fishes.

Prosser and Brown (1962) reported that fish approximately double their oxygen requirements for every 10°C rise in temperature. Thus, it is important from the standpoint of total metabolic expenditure for fishes to enjoy acclimation in gradients of both temperature and dissolved oxygen. According to Brett (1944), however, acclimation from 3.9° to 13°C took approximately 20 days in the goldfish *(Carassius auratus* Linnaeus), and may have been even slower for the reciprocal gradient. To compensate the need for continuous acclimation, fishes seek optimum temperatures (at which metabolic oxygen demand is probably also optimum) and tend to congregate there (Dendy, 1945, 1946; Buck and Cross, 1952; Brett, 1944; Fry and Hart, 1948a, b). Preferred temperatures have been determined for a relatively few fish species (Fry and Hart, 1948a), and not at all for the black bullhead. Morris (1965), opposed to Brett's (1944) observation, noted that *I. natalis* adjusted rapidly to different acclimation temperatures by invoking compensatory metabolic adjustments. When moved to water at 27°C, a fish acclimated at 12°C, lowered its metabolic level from 0.35 to 0.15 ml O_2/hr.

Active metabolism of some fish *(Salvelinus* sp.) may be four times the resting rate (Fry and Hart, 1948a). The activity patterns and distributional success of fish were most often reflected by their metabolic rate. For example, percid darters have several times greater metabolic rates than most sluggish fish (Vernberg, 1954).

Caillouet (1967a) concluded that death of channel catfish following hyperactivity was caused, at least in part, by lactic acidosis. However, Black (1955) and Caillouet (1967b) suggested that increased blood lactic acid in exercised black bullheads was insufficient to cause this condition. Black (1955) attributed this to a low Bohr Effect, i.e., increase in blood lactic acid had little effect on the oxygen combining capacity of the blood. Buddenbrock (1938) suggested lactic acid concentration might lead to tissue hypoxia. Thus fish with relatively low metabolic requirements, enjoying the advantage of a low positive Bohr Effect, should be favored in situations where the dissolved oxygen-carbon dioxide ratio imposes hypoxial limits on less favored species.

Early studies by Birge (1907) showed that waters in which dissolved oxygen was abundant produced no gas other than carbon dioxide in appreciable amounts. McCay (1925) and Powers (1937) implicated carbon dioxide in fish poisonings. This gas is important from the standpoint of its relation to gas exchange at the gills – since it cannot be excreted osmotically against a gradient – and in its relationship to the oxygen combin-

ing capacity of the blood and the premature unloading of oxyhemoglobin (Matthew, 1921). W.G. Moore (1942) measured the oxygen regimens of 13 species of fish by suspending them in live boxes at various depths. Black bullheads were the least susceptible to hypoxia at the highest carbon dioxide tensions encountered. Even the brown bullhead was unable to endure oxygen tensions of 2.8 to 3.7 ppm for 24 hours in waters of high carbon dioxide tension. Powers, et al. (1938) showed that fishes could absorb oxygen to low levels in wide ranges of carbon dioxide. The species *Micropterus dolomieui* Lacépède, *Ambloplites rupestris* (Rafinesque) and *Perca flavescens* (Mitchill) were able to extract oxygen down to 0.30 and 0.40 ml/l in carbon dioxide tensions of 0.15 to 21.00 mm Hg. Comparable data for ictalurid fishes have not been presented.

Natural mortality for a given body of water, and species complex, during a specific period of time, appears to be one of the most difficult of all fish population parameters to estimate with any degree of statistical accuracy (Ricker, 1944, 1958; Regier, 1962). Two basic analysis procedures have been proposed and subsequently elaborated to provide mortality estimates. The first provides estimates for populations that obey certain well-defined restrictions: the population must remain unexploited throughout the study period; it must be affected by neither recruitment nor emigration; it must be assumed homogeneous with respect to species and age. The second method is designed to provide estimates for exploited populations and becomes rather involved by comparison. It is not surprising, then, that few attempts have been made to estimate differential mortality in freshwater situations. It is usually difficult to observe a population in extensive enough detail to assure than the necessary assumptions have been met. As a result, most of the mortality that has been reported has been of the chance observation type; however, even this type of information can prove important to the management of a fishery (Bailey, 1955).

Bennett (1948) sampled Gale Lake, Illinois, previous to and after a known winter-kill during which approximately 80 per cent of the population was decimated. Analysis of the persistent population pointed to a conclusion now basic to fisheries management; population mortalities are seldom, if ever, complete, and the remaining portion can radically alter the fishery condition. Gale Lake bullheads, along with carp and buffalofish, survived the mass-mortality, and subsequently proliferated to such an extent that the lake no longer provided sport fishing. Powers (1937) commented on the factors involved in the sudden mortality of fishes, relating the aperiodic influence of bacterial oxygen depletion-carbon dioxide elevation curve to unexplained fish kills, and conjectured "derangement" resulting from continuous adjustment to different carbon dioxide tensions as an important mortality factor.

MATERIALS AND METHODS

Study Area Characteristics

Sample populations utilized during this study were contained within the adjoining central Kentucky counties of Madison, Fayette and Clark in the Kentucky River drainage. The area is underlain by Ordovician and Silurian limestone (Hall and Palmquist, 1960). Elevation ranges from 500 feet on valley floors to as much as 1,000 feet on ridge-tops on shale and limestone hills; major drainages range in elevation from 800 to 900 feet. Graybrown podzolic soils underlain by soft limestone or highly calcareous shale are conspicuous on steeper ridges (Austin, 1965).

The continuity of underlying strata lends some degree of similarity to major streams and artificial impoundments throughout the area, but differences in topography and land-use patterns affect stream habitats and the faunal complexes they contain. Consequently, several streams were surveyed before the study areas listed below could be chosen. Since it was desirable to compare certain data from different habitat types, the bullhead populations of Wilgreen Lake and several smaller impoundments were also utilized.

Streams:

Streams throughout the study area were surveyed to ascertain the character of their bullhead populations. Two of these, Boone Creek in Clark and Fayette counties, and Strodes Creek in Clark and Bourbon counties, were considered to have suitable bullhead populations. The Boone Creek drainage consists of first through fifth order streams from its headwater just north of U.S. Route 60 to its confluence with the Kentucky River, 0.8 km east of Clay's Ferry, Kentucky. Land adjoining lower order streams (first through third) was being utilized primarily as permanent pasture, with only a small portion under crop tillage. Third order streams contained numerous silt bottom pools that proved excellent habitats for isolated populations of black bullheads. Two third order tributaries, the East and West forks of Jones Creek, which converge approximately 10 km from the intersection of Cleveland and Sulfur Well roads, were sampled through the study period.

Strodes Creek, located north of Winchester, Kentucky (38° 02' latitude; 84° 12' longitude), is a tributary of Stones Creek which, in turn, flows into the South Fork of the Licking River in Bourbon County. The entire southern drainage joins the main fork of the Licking River at Falmouth, Kentucky. The streams in this drainage, especially Strodes Creek and its tributaries, are maximally influenced by agricultural use. Meandering stream beds are extensively silted, pools are abundant and stream flow is minimal during most of the year. All tributaries sampled contained large numbers of black bullheads. Johnson Creek, the most prominent tributary of Strodes Creek, was sampled during the spring and summer of 1971.

Ponds:

Farm ponds, and other small earthen impoundments, were surveyed to determine the feasibility of their use for this study. Seventeen ponds were considered; of these, the five listed below were found to contain black bullhead populations and were selected for further study. Ponds I, II, and III were located on the Central Kentucky Wildlife Management Area situated 4.2 km east of Kingston, Kentucky (37° 38' latitude; 84° 14' longitude). Pond IV was located on Fairview Farm approximately 2.4 km south of the intersection of state routes 1156 and 25 near Whitehall, Kentucky. Pond V was in Fayette County, Kentucky, 0.8 km south of state route 421 at 37° 54' latitude; 84° 20' longitude.

Pond I: This pond had a surface area of approximately 0.65 acre (.26 ha), with a maximum spring depth of 2 m. The entire surface area was of open water; no marginal or emergent vegetation occurred. The pond accepted run-off from a denuded 3.0 acre barnlot.

Pond II: Formed within a natural valley approximately 0.4 km wide, this pond had a surface area of 0.5 acre (.20 ha) and a maximum depth of 2.6 m. It received a spring-fed stream which flowed throughout the study period. Emergent vegetation (primarily *Sagittaria* sp. and *Scirpus* sp.) and mats of filamentous algae *(Spirogyra* sp.) covered approximately 25 to 30 per cent of the surface through spring and summer. The bottom deposits consisted of pulpy peat and muck that reached depths of 0.9 m.

Pond III: This pond was small and shallow, with a surface area estimated at 0.125 acre and maximum spring depth of 1.0 to 1.2 m. It was located within a natural depression that contained some water throughout the year, but received the flow from adjoining pastures only during heavy rains. Emergent vegetation (predominantly *Sagittaria* sp.) was prominent over the entire surface.

Pond IV: With a surface area of 0.50 (.20 ha) acre and a maximum depth of 1.5 m, this pond also drained pastured areas. Aquatic vegetation was limited to insignificant accumulations of pondweed *(Potamogeton* sp.); however, during spring and early summer it was extensively covered with algal mats *(Spirogyra, Oedogonium* and *Zygnema).* Bottom deposits were of ooze to a depth of 1.0 m.

Pond V: This was a pond of recent origin (four years) located at the base of a natural valley. The open water area covered approxi-

mately 0.25 acre (.10 ha) acre, and the maximum spring depth was 1.5 m.

Lakes:

Wilgreen Lake, formerly known as Taylor Fork Lake, is located in Madison County, Kentucky, with spillway and access point located approximately 4 km from the intersection of Barnes Mill and Curtis roads (37° 54' latitude; 84° 20' longitude). The lake has been inadequately surveyed surveyed; consequently most morphometric data has not been detailed. The shore line extends an estimated 42 km, containing 175 surface acres of water (71 ha). The early spring maximum depth was between 24 and 26 m. Shoal areas (water less than 1.2 m deep) comprised an estimated 15.0 to 20.0 per cent of the total area: aquatic vegetation, other than filamentous algae, was conspicuously lacking from shoal waters. Wilgreen Lake was sampled during the period July 1970 to June 1971.

Capture Methods

Several methods were employed to capture specimens. Most pond sampling was during winter months (Nov. 1970 to Feb. 1971) using wire traps. Larvae and young-of-the-year were sampled by means of a modified meter net, and by hand netting along shore-lines. Stream populations were sampled with a 15 foot (4.57 m) common-sense seine of 1/4 inch (6 mm) linear mesh. Samples were taken from Wilgreen Lake during the fall of 1970, and from February through June 1971, using: 5-cm inner mesh trammel nets established across major channels; wing nets, 3.8- and 2.5-cm mesh funnels and 1.3-cm wings, fished in waters less than 3 m deep: bag seines trawled in affluents and shallow coves: and 230-volt electric shockers operated along shore.

Population Dynamics

Food Habits. Food habits were assessed for all populations studied, i.e., from ponds, lakes and streams, and for all age groups within the populations. The terminology of Hubbs (1943) for establishing age classes was followed. According to this analysis, transition from lower to higher age class occurs on either January 1 or July 1 (Hile, 1948). Since the black bullheads in this study were found to form annuli during the month of June, July 1 was used as the transformation date.

To determine feeding selectivity, benthic and planktonic analyses were carried out during all seasons of the year, and the results scaled to reflect annual availability. The weighted percentage of availability was then compared to percentage estimates of appearance of the same items in the stomach contents of representative samples to form an electivity ratio for each item. The electivity ratio used by Priegel (1970) is represented by the equation:

$$E = \frac{r_i - P_i}{r_i + P_i}$$

Where r_i is the relative percentage of any food item in the stomach, and P_i is the relative percentage of the same item available to the fish.

Values of (E) range from −1 to +1, and a value of 0 was expected for a food item when no selective process was operative. Invertebrate identification followed Eddy and Hodson (1961) and Pennak (1953).

Age and Growth. Representative samples from all study areas were investigated to determine age and growth characteristics. Age determinations were made by modifications of procedures suggested by Lewis (1949) and Sneed (1951). Lewis aged black bullheads by viewing the annular markings on vertebral centra, and Sneed was able to age channel catfish by the number of annular depositions on pectoral and dorsal spines. In the latter case, these sections were made near the base of spines, a drop of xylol added, and the preparation viewed under indirect light. In this study a more facile modification of Sneed's procedure was successfully employed. Instead of making a thin section, the pectoral spine was simply severed near its base with a high-speed rotary cutter (Dremel Model 42), the cut portion polished if necessary by the use of a high-speed jeweler's stone, and the entire spine mounted in styrofoam for observation under

indirect light. Age estimates, when compared to preparations by Sneed's method (1951), were identical.

Total length (tip of snout to tip of tail) and a standard length (tip of snout to the flection point at the caudal peduncle) were determined on a standard mm-measuring board. All weights were determined on a tri-beam balance permitting a precision of ±0.05 g.

The coefficient of condition (K) was determined for representatives of pond, lake and stream populations. The condition factor was that proposed by Hile (1936), represented by the equation:

$$K = \frac{100W}{L^3}$$

where, K is the coefficient of condition, W is the weight expressed in grams and L is the standard length expressed in centimeters.

Since the coefficient of condition was designed as a comparative value, it has little significance as an absolute number.

Weight-length relationships for each habitat were determined according to the expression Log W = a + n Log L, where W is the weight in grams and L is the length in millimeters. The resultant regression equations were analyzed as to the homogeneity of their slopes. In addition, correlation coefficients were employed to establish the relationships between weight and length, age and weight, and age and length for each population.

Population Estimates. Population estimates were made for pond populations to relate degree of crowding and intraspecific competition to population success. These estimates were made by employing the mark-recovery procedure detailed by Fredin (1950) which modifies the Peterson method by considering each sample as a separate estimate. By this method, usually referred to as a Schnabel estimate (Ricker, 1975), a more accurate estimate is assured by the process of minimized squares according to the expression (where marking is continued into the recapture period):

$$N = \frac{S\, n^2 (m + u)}{S\, (nm)} \qquad (1)$$

where, N is the total population estimate, m is the number of fish marked during the first sampling period, u is the number of unmarked fish in the second sample, n is the number of marked fish in the pond, and S represents summation.

Ricker (1958) noted that (1) was most efficient when the value n/N was 0.5. Where this assumption could not be made, and in cases where subsequent estimates were made over long periods of time (one month or more), the standard Petersén mark-recovery index was utilized (valid only if M is constant). According to this procedure, the total population (P) is equal to a ratio of the number of marked and unmarked fish in a pond according to the expression:

$$P = M (U + R)/R$$

where, M is the number of fish marked during the first sampling period, U is the number of unmarked recoveries and R is the number of marked recoveries.

Natural Mortality. The bullhead population in Pond I was followed throughout the study period to set limits on the extent of natural mortality, and to determine the period or periods when fish are most vulnerable to the factors of natural mortality. The procedure used to calculate natural mortality followed those of Regier (1962) for exploited populations, and will not be detailed here. Although this pond was not exploited through fishing effort, sampling in the pond was considered exploitation, and the mortality was analyzed accordingly.

Reproductive Potential

Gonadal Development. Fish were removed from Pond I and II during the period August 1970 through July 1971 to obtain an index for male and female gonad development after procedures suggested by Larimore (1957). Since Dennison (1970) established gonad development curves for male and female black bullheads in a lake population, greater emphasis was placed on pond

development during this study. However, estimates were made throughout the spring and summer of 1971 for lake and stream populations, and the results were superimposed on pond fish curves. The gonadal development index is simply a ratio of gonad weight to body weight. Samples from ponds were analyzed at bi-weekly intervals from August 1970 through February 1971, and weekly thereafter. From these values the high and low points of the reproductive cycle were determined. In addition, gross morphology of the gonads was described for each stage in the development sequence.

Fecundity. The several methods used for analysis of egg production in fish (Davis and Paulik, 1965; Boyar and Clifford, 1967; Behmer, 1969; Larimore, 1957) can be grouped under three headings: dry weight measure, volumetric measure, and egg displacement. Each of these methods was analyzed in contrast to total egg counts to determine the most suitable method for bullhead fecundity determinations (Table I). Subsequently, all determinations were made by the egg-weight and displacement methods of Burrows (1951b); the dry-weight method was excluded. Since all methods tested overestimated the actual number of eggs (minus any adhering germinal tissue), all determinations were corrected by factors corresponding to the magnitude of over-estimation. Displacement determinations were multiplied by a factor of 0.90, volumetric methods by 0.79, and egg-count determinations by a factor of 0.98 (Table I) to account for adhering germinal tissues. All weights obtained during this procedure were determined by means of a Mettler 400 analytical balance with ±0.0005 g precision.

Induced Spawning. Eight pairs of black bullheads, designated as possible spawners, were brought into the laboratory and segregated into breeding pairs. The fish ranged in weight from 130 to 145 g, and in standard length from 168 to 220 mm. They were maintained on a diet of adult crayfish reinforced with liver. The male and female of each pair were separated from each other in 50-gallon (189 l) aquaria by imposing 1.25 cm mesh weld-wire partitions. The photoperiod was varied according to the environmental photoperiod, and temperature was increased at the rate of 1°C per day to a maximum of 27°C.

In accordance with a procedure detailed by Sneed and Clemens (1960), each pair was treated with dried carp pituitary which had been previously prepared by desiccation in four 12 hour changes of acetone, then stored in sealed vials. Each fish received 4.0 mg dried pituitary per 24 hour period until signs of pre-spawning behavior appeared, or for a total of 10 intramuscular injections. Pituitary glands used in the study were obtained from carp seined or trapped in local streams; these were not separated as to sex or stage of reproductive development. Pituitaries used were not over two hours old when dried.

Physiological Ecology

Oxygen Consumption. Oxygen consumption rates were determined for age groups post-larva through age group I (to formation of second annulus) at three acclimation temperatures, 7°, 12° and 23°C. Acclimation was accomplished for each group by subjecting ten or more fish to progressively decreasing temperatures in a Sherer-Gillett Environmental Chamber. Once the desired temperature was reached, fish were held at this temperature for an additional 7 to 10 days. Notably, however, post-larval specimens (approximately 2 days post-hatching) could not be acclimated to 7°C. Consequently, determinations for this group were made only at 12° and 23°C.

Oxygen consumption rates (standard rates) were determined by immersing fish held in weld-wire cages consistent with their total length, into 5.54 liter glass aquaria. The aquaria were sealed with a plexiglass cover and silicon sealant, and filled to capacity through a single 7.5 mm hole drilled to accept the BOD probe from a YSI Model 54 Oxygen Analyzer. Subsequent to filling, fish were allowed to accustom themselves until locomotory activities minimized before initial oxygen readings were made. Prior to each experimental run, demineralized water in the chambers was recharged with oxygen to a level of 8.0 to 9.0 ppm. (Oxygen con-

Table 1. Preliminary analysis of egg count methods. Column A= total counts; Column B= estimation by displacement methods; Column C=estimation by volumetric methods; Column D= individual egg weight method. SL= standard length (mm); D= deviation from total count; $\overline{X}$= mean of deviations.

		A	B		C		D	
SL	LOCATION	TOTAL COUNT	ESTIMATE	D	ESTIMATE	D	ESTIMATE	D
169	POND	1891	1923.0	+32	2312.5	+493.5	1900	+9
176	POND	1927	1985.0	+59	2404.0	+477.0	1943	+16
176	POND	1914	1922.0	+8	2322.0	+408.0	1923	+9
210	POND	2880	3845.0	+965	3520.0	+640.0	2992	+112
156	POND	1600	1748.0	+148	2104.0	+405.0	1623	+23
195	POND	2880	3312.0	+432	3415.0	+535.0	2903	+23
177	POND	3015	3150.0	+135	3271.0	+156.0	2975	+40
		$\overline{x}$ = 2301.0	$\overline{x}$ = 235		$\overline{x}$ = 473.4		$\overline{x}$ = 33	
			% dev = 10.21		% dev = 20.54		% dev = 1.75	
		Correction Factor =	100 - .1021 (.90)		100 - .2057 (.79)		100 - .0175 (.98)	

sumption rates were read in mg O_2/g/hr for purposes of comparison.) Consumption rates at the three acclimation temperatures were expressed as functions of stage of development, and the corresponding Q_{10} values between each pair of acclimations were established according to the equation of Prosser and Brown (1962). In addition, oxygen consumption per fish was expressed as a function of weight at 23° and 12°C. For age groups with weight ranges greater than two standard errors of mean weight, consumption rates were converted to the rate of an individual of mean weight according to the equation:

$$M_m = (W_m^a \times M)/W^a$$

Where, M_m is the metabolic rate of a mean weight fish, W_m is the mean weight, M is the metabolic rate of any fish in the sample, W is the weight of any fish in the sample, and a is the slope of the weight versus consumption rate curve for any size group (Smit, et al., 1971).

In addition to routine rates, oxygen consumption was measured as a function of decreasing oxygen tension and increasing carbon dioxide tension in order to establish threshold values. Water used for these procedures was first "stripped" of oxygen down to 4.0 ppm (2.8 ml/l at 20°C) by subjecting it to a jet of nitrogen gas. Fish were then allowed to spontaneously reduce oxygen levels to near-asphyxiation levels. Rates were continuously monitored by a procedure analogus to that described above.

Temperature. Lower incipient lethal temperatures, critical thermal maxima and temperature preference ranges were determined at the three acclimation temperatures listed above. Lower lethal temperatures were established by subjecting groups of ten or more fish (post-larva through age II) to progressively high temperatures from a minimum corresponding to the freezing point of water. The point in time at which 50 per cent mortality (LT_{50}) occurred was recorded, and the temperature at which no further death occurred with time was considered the lower lethal temperature. While under observations the fish were disturbed only for periodic aeration of the water.

Critical thermal maxima (incorporated into the data analysis as upper lethal temperatures) were determined by a procedure similar to that described by Hutchinson (1961). Tri-necked distillation flasks were fitted into hemispherical heating mantles which could be heated at any desired rate by means of a variable voltage transformer. Animals to be tested were placed in sufficient demineralized water to allow free movement. Alternate ports of the flask were provided with an air hose to aerate and circulate the water, and the probe from a YSI Model $4S_2$ Tele-Thermometer. Temperatures were recorded at the beginning of each run (t_o) and at the CTMax (t_f), which was the point at which an animal failed to maintain an upright position. All animals used for CTMax determinations were acclimated at 7°, 12°, and 23°C for periods of 7 to 10 days. Subsequent to determination, the previously unfed animals were allowed to recover in water held at their prior acclimation temperature.

Temperature preference ranges were determined for age groups post-larva through age I, since design of the apparatus did not facilitate the handling of older fish. Animals previously acclimated to the temperatures designated above were placed in a 10-foot galvanized gradient chamber. The chamber, located in a walk-in refrigerator of 5° ambient temperature, was so constructed that temperature could be graduated from 3° to 27°C through 12 previously marked intervals. Ten to fifteen animals of comparable age and size were placed in the chanber at the point corresponding to their prior acclimation temperature. At hourly intervals, for a total of nine hours, the animals were observed and their positions in the gradient recorded. This was easily accomplished without causing disturbance, since the fish could be observed from outside the refrigerator. In order to eliminate light as a factor in range selection, determinations were made under full illuminations on fish previously acclimated to constant light.

Correlative Studies. In conjunction with laboratory and field studies, water chemistry analysis was accomplished for each habitat sampled following Hach Chemical Company procedures. Table 2 contains a complete listing of determinations, and the range of each year specified periods of time.

Statistical analyses followed the procedures of Sokal and Rohlf (1969), and Downie and Heath (1961).

RESULTS

During the period July 1970 through July 1971, a total of 623 adult black bullheads (age groups I through VI) was taken from the study area. Fifty-six per cent of these (349 specimens) were obtained from ponds, 36% (224 fish) from streams, and the remaining 8% (50 fish) from Wilgreen Lake. In addition to adults, 300 post-larvae and juveniles were taken from the three habitat types.

Food items consumed by 292 adult black bullheads, the availability of each item in the habitat expressed as a weighted volume per cent, and the corresponding electivity ratio of each, are presented in Table 3. Although a great variety of food items was taken by adults, there was evidence to suggest feeding selectivity. Table 3 shows that chironomid larval and pupal stages made up a predominant part of the adult diet; however, this item had no greater selection value (0.1 to 0.5) than some other less common foods.

Food items taken most frequently differed from one habitat to another. Pond populations took chironomids and additionally relied heavily on physid and

Table 2. Water chemistry analysis of ponds I, II and IV, Wilgreen Lake and Boone Creek for the months indicated within the period, June 1970 through July 1971. All concentrations are in averages and ranges expressed as parts per million (PPM). Temperature is expressed in° C.

	Period of Observation	D.O.	CO_2	Methyl Orange Alk.	T Hardness (ppm $CaCO_3$	pH	Turbidity	H_2S	NH_3 Nitrogen	Temp. °C
BOONE	April, 71	9.8-13.4	0-2.0	132-200	152-206	8.0-8.9	0.5-7.5	*	*	16-21.5
CREEK	May, 71	9.8-12.6	0-7.0	116-172	160-238	6.4-6.9	0.5-6.8	*	*	17.5-23.0
	June, 71	6.8-11.2	0-2.0	130-164	182-195	6.5-7.5	3.0-10.2	*	*	19.0-26.0
WILGREEN	March, 71	11.5-13.0	5.0	*	*	6.0	*	*	*	5.5-8.9
LAKE	April, 71	10.0-13.0	5.0	*	*	6.5	*	*	*	9.0-15.6
	May, 71	2.3-10.2	5.0	82-134	120-165	7.0	4.0-7.2	0.1-1.5	0.7-0.9	15.0-25.5
	June, 71	0.4-11.7	5.0	62-146	106-175	6.5-6.9	4.0-20.0	0.2-0.5	0.6-1.0	18.0-30.0
POND I	June, 70	4.9-7.7	5.0	84-88	84-88	6.5-6.8	140	0.2	1.04	18.5-25.0
	July, 70	3.9-6.0	7.4	84-94	96-116	6.2-6.9	100	0.3	1.66	25.0-29.0
	August, 70	3.0-6.8	9.4	84-102	90-116	6.0-6.9	100	0.4	1.78	25.0-29.0
	September, 70	3.9-6.0	8.4	88-102	48-90	5.4-6.3	84	0.2	1.60	23.2-29.0
	October, 70	8.0-12.0	7.3	66	56-92	5.4-6.0	84	0.2	1.08	14.5-20.2
	November, 70	10.0-13.5	5.0	82	58-88	6.0	84	0.1	0.70	9.5-14.8
	December, 70	10.5-14.0	5.0	*	*	7.0	*	* *	*	6.0
	January, 71	14.0	5.0	*	*	7.0	*	*	*	5.0
	February, 71	14.0	5.0	*	*	7.0	*	*	*	4.0-5.0
	March, 71	13.5-14.0	5.0	70	76	6.5-7.0	76	0.0	0.00	5.0-9.0

	Period of Observation			Methyl Orange Alk.	T Hardness (ppm $CaCO_3$	pH	Turbidity	H_2S	NH_3 Nitrogen	Temp. °C
	April, 71	9.3-10.4	5.0	84	140	6.0-6.2	80	0.1	0.30	9.0-13.0
	May, 71	8.5	15.0	84	148	6.2	85	0.0	1.78	13.0-17.0
	June, 71	4.7	7.5	84	140	5.8-6.5	80	0.2	1.78	17.0-28.0
POND II	June, 70	8.9-10.0	5.0	88	112	6.5	12	0.0	0.20	16.2-19.0
	July, 70	7.5-9.0	5.0	84	100	6.5	19	0.0	0.20	17.8-21.0
	August, 70	6.0-8.5	5.0	84	96	6.0	23	0.0	0.30	19.4-23.5
	September, 70	6.5-8.5	5.0	88	100	6.5	25	0.0	0.10	17.5-26.0
	October, 70	12.5	5.0	84	92	6.0	12	0.0	0.00	16.8-23.5
	November, 70	13.5	5.0	84	92	6.0	15	0.0	0.00	12.9-17.0
	December, 70	14.2	5.0	*	*	6.2	*	*	*	7.4-12.0
	January, 71	14.0	5.0	*	*	6.0	*	*	*	6.5
	February, 71	13.8	5.0	*	*	6.5	*	*	*	5.5
	March, 71	12.5-14.0	5.0	102	122	6.2-6.9	31	0.0	0.00	6.0-10.0
	April, 71	10.9-13.0	6.0	88	100	6.0-7.0	19	0.0	0.00	10.0-15.0
	May, 71	9.5-12.5	5.0	84	96	6.0-7.0	19	0.0	0.10	10.0-15.0
	June, 71	8.5-11.9	7.4	90	100	6.5-7.2	19	0.0	0.10	19.0-26.0
POND IV	April, 71	6.3-7.5	8.5	*	*	7.0	104	0.5	0.75	*
	May, 71	4.9-5.5	11.7	*	*	5.8	112	0.5	1.35	*
	June, 71	2.5-4.9	14.0	*	*	6.0	140	0.5	1.78	*

* not determined

Table 3. Food consumption of 292 adult black bullheads expressed as (A) percentage of total complement, (B) represents percentage of each item available and (C) is the electivity value of each available item.

Food Organism	Ponds			Wilgreen Lake			Streams		
	A	B	C	A	B	C	A	B	C
Annelida									
Oligochaeta	6.1	1.5	0.6	8.8	3.5	0.4	2.9	1.9	0.2
Pelecypoda									
Spaeriidae	3.2	12.4	-0.6	0.4	7.4	-0.9	13.1	15.3	-0.1
Gastropoda									
Planorbidae	2.1	0.8	0.5	2.8	5.5	-0.3	2.9	1.4	0.4
Physidae	5.5	0.8	0.7	16.0	5.5	-0.6	5.8	6.4	-0.1
Rotifera	0.0	3.2	-1.0	0.0	7.8	-1.0	0.0	*	...
Cladocera	0.0	9.3	-1.0	0.0	12.5	-1.0	0.0	*	...
Copepoda	0.0	6.5	-1.0	0.0	3.5	-1.0	0.0	*	...
Ostracoda	0.0	1.3	-1.0	0.0	7.8	-1.0	0.0	*	...
Amphipoda	1.4	2.5	-0.3	4.9	1.7	0.4	2.9	5.3	-0.3
Isopoda	0.0	1.1	-1.0	0.0	0.3	-1.0	0.7	0.5	0.2
Decapoda	1.5	1.5	0.0	0.0	0.6	-1.0	5.1	7.8	-0.2
Ephemeroptera	1.5	0.3	0.6	1.1	1.1	0.0	3.6	2.9	0.1
Plecoptera	0.0	0.0	...	0.0	0.0	...	1.5	1.1	0.2
Odonata									
Zygoptera	3.0	2.1	0.2	4.2	1.1	0.6	0.7	2.0	-0.5
Anisoptera	6.7	1.5	0.6	2.1	1.9	0.1	3.6	3.0	0.1
Trichoptera	0.0	0.0	...	0.0	0.0	...	3.6	2.9	0.1
Diptera									
Chironomidae	47.2	45.2	0.0	55.5	19.3	0.5	39.0	11.9	0.5
Tabanidae	2.3	0.6	0.6	0.0	0.5	-1.0	0.7	0.1	0.7
Tipulidae	0.0	0.0	...	0.0	0.0	...	3.6	0.7	0.7
Simulidae	0.0	0.0	...	0.0	0.0	...	8.0	2.9	0.5
Unidentified	2.0	0.8	0.5	4.9	1.4	0.6	0.0	0.0	...
Hemiptera Corixidae	0.0	0.8	-1.0	0.0	0.9	-1.0	2.2	1.4	0.2
Amphibia									
Ranidae (Larva)	1.5	1.8	-1.0	0.0	0.0	...	0.0	*	...
Pisces									
Lepomis macrochirus	3.8	5.6	-0.2	0.0	*	...	3.6	3.6	0.0
Micropterus salmoides	2.3	0.5	0.7	0.0	*	...	0.0	*	0.0
Pimephales promelas	13.0	7.8	0.3	0.0	*	...	2.2	1.0	0.4
P. notatus	0.0	0.0	...	0.0	*	...	2.9	4.6	-0.3
Cyprinus carpio	0.0	0.0	...	0.0	0.0	...	0.7	0.2	0.7
Notropis sp.	0.0	0.0	...	0.7	*	...	8.0	7.4	-0.4

* Density Not Determined

planorbid snails, sphaeriid clams, dragonflies and the young of fish species (especially the minnow *Pimephales promelas*). Adults from Wilgreen Lake consumed appreciable numbers of the amphipod *Hyalella*, larval damselflies, physid snails and oligochaetes. Adults taken from streams consumed a wider range of food items than did populations in either lake or ponds, but still relied heavily (39%) on chironomids. Although of lesser importance, tipulid and simulid larvae, decapod crustaceans, mayflies, sphaeriid clams and physids were found more frequently than other food items. Fingernail clams (Sphaeriidae) formed a notable portion of the food consumed in ponds and streams, but appear to have been selected against in both situations. A predominant percentage of stomachs investigated contained some filamentous algae (181 of 282: 64%) from March through May, but this item was not considered in Table I because its true significance as a food item was not determined.

Adult feeding changed markedly with season. According to our observations, from a peak during late spring, feeding diminished with the progression of summer, increased again in early fall, and appeared to cease entirely during winter months. The stomachs of 31 fish captured from ponds during 15 December 1970 to 1 February 1971 contained no food. Wire traps used to capture these specimens were usually left unraised for 12-hour periods; however, peptic digestive rates during winter are sufficiently low (Nordlie, 1966; Baur, 1968) that some food should have remained if the fish were actively feeding. Measurable quantities of food did not appear in the stomachs until mid-March, corresponding to temperature increases above 10°C.

Larval and juvenile feeding appeared even more selective than that of the adults. Table 4 lists the food items consumed by 68 larval bullheads from Wilgreen Lake and Pond I. Since larval food analysis was not accomplished for stream populations, these data are not comparative. They did indicate, however, that food was selected far more closely according to its position in the habitat than its relative size.

TABLE 4. FOOD ITEMS OF 68 LARVAL BULLHEADS: COLUMN A= EACH ITEM AS PERCENT OF TOTAL FOOD COMPLEMENT: COLUMN B= THE AVAILABILITY OF EACH ITEM AS PERCENT OF TOTAL: AND COLUMN C= THE ELECTIVITY RATIO.

Food Organism	A	B	C
Rotifera	1.8	12.5	-0.8
Cladocera	4.8	14.3	-0.5
Copepoda			
Copepodids	6.0	3.6	0.3
Nauplii	2.2	23.1	-0.8
Ostracoda	48.0	9.0	0.7
Amphipoda	34.0	8.0	0.6
Diptera			
Chironomidae	1.4	22.0	-0.9
Annelida			
Oligochaeta	0.1	4.1	-1.0
Nematoda	0.1	3.0	-0.9
Miscellaneous	1.2	*	....

* Density not determined

In both habitats sampled, ostracods, amphipods and adult copepods made up the bulk of the diet. Pond larvae relied more heavily on copepods than their lake counterparts, apparently because of the differential abundance of ostracods and amphipods between the two areas. Nauplii, the most abundant planktonic component, and chironomid larvae, the most prevalent benthic food, were strongly selected against. In addition, selection against other benthic elements seemed to support the observation that most larval feeding was pelagic.

Larval feeding was observed on several occasions during July and August 1970 and June and July 1971. Aggregations consisted of curious admixtures of different aged individuals. Approximately 25 to 30 % of the pods observed during June 1971 consisted of yolk-sac stages (determined from capture percentages) which according to the time required to absorb the yolk, were considered two to three days younger than the others. Forming aggregations did not begin feeding immediately, but continued to wander until a visual orientation pattern was achieved. Pods observed in Wilgreen Lake were always oriented on an axis facing the shoreline. Once disturbed, the larvae broke up into less compacted masses, submerged and swam toward open water, where they regrouped on the same imaginary axis. Feeding appeared to be restricted to a limited area

about the axis of orientation, and continued at the surface during daylight hours. Larvae were always found in the few areas where aquatic vegetation and floating algal mats were most prominent. Most observed feeding was at the water surface. However, the inclusion of annelids, free-living nematodes and chironomid larvae in the stomach contents suggested that some bottom feeding also occurred.

The mean ponderal indices for adult fish sampled from each habitat during April, May and June 1971 were: ponds, (54 fish) K = 2.55, standard error 0.38; Wilgreen Lake, (23 fish) K = 3.00, standard error 0.51; streams, (32 fish) K = 2.50, standard error 0.49. The K factors were comparable for bullheads from the three habitats; a two-way analysis of variance indicated that no significant difference occurred at the 1.0 per cent level of confidence (F = 132.50/−2.31).

Weight-length relationships from more extensive sampling (372 specimens) throughout the study period were established. The relationship for 167 pond specimens (age groups I through VI) fit the equation: Log W = −4.8498 + 3.1135 Log L; the relationship for 45 Wilgreen Lake bullheads of comparable age was Log W = −4.1812 Log L; and the same relationship for 100 stream specimens was Log W = −2.4453 + 1.9968 Log L. An analysis of homogeneity of slope for the three regression curves indicated significant differences in the weight-length relationship at the 1.0 per cent level (F_s = 29.6948/$F_{2,103}$ = 4.82). The correlation between growth in length and weight was particularly high for ponds (r = 0.94) and Wilgreen Lake (r = 0.97), but not for streams (r = 0.68).

The length-weight curve illustrated in Fig. 1 represents pond, lake and stream populations and is interpolated to express the wieght at a point where length approaches zero. The curves in Fig. 2 illustrate mean

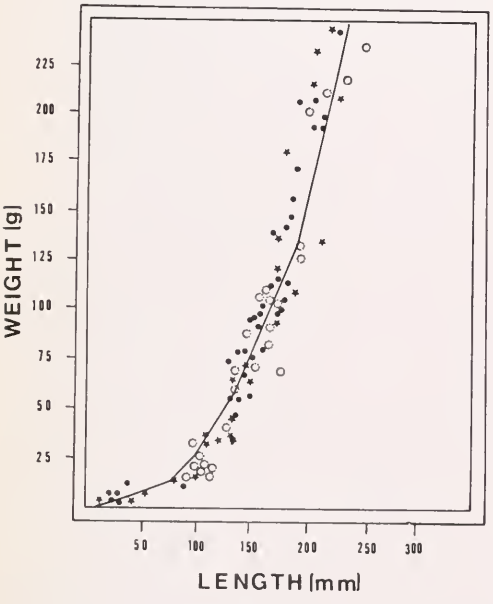

Figure 1. Length-weight relationships of 372 adult black bullheads from pond 2, Wilgreen Lake and Boone and Johnson creeks. Curve extrapolated to the point where weight approaches zero. Solid circles=ponds; solid stars=lake; open circles= streams.

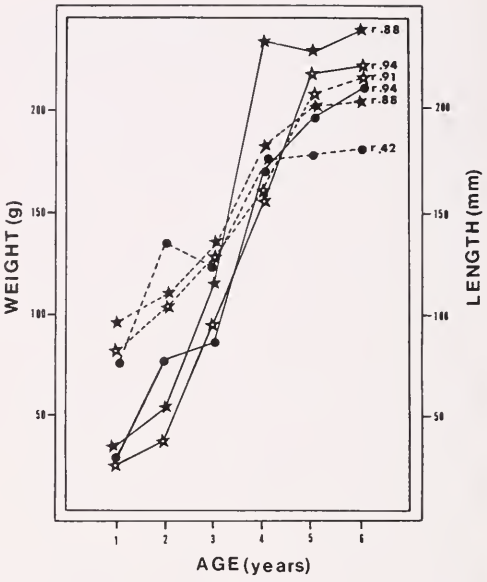

Figure 2. Mean weight and length at the time of annulus formation of 372 adult black bullheads (age groups I-IV) for ponds, lakes and streams. Each curve accompanied by a coefficient of correlation (r) computed using all measurements about the line indicated. Dashed lines=length versus age; solid lines=weight versus age; solid circles=ponds; open stars=lake; solid stars=streams.

weight and mean length (mm) as functions of age at the time of each annulus formation. Each curve is accompanied by a corresponding coefficient of correlation computed for all measurements within the range. In computing these data, July 1 was taken as the date of annulus formation (year class I), although experimental evidence indicated that most black bullheads (27 to 31 or 87 per cent) formed the annulus before the third week in June.

Correlation between growth in length, growth in weight and age in years, as indicated in Fig. 2, are quite variable among the three habitats. The most rapid growth rates were apparent in the Wilgreen Lake and stream populations, which also had the most favorable length-weight relationships and mean ponderal indices for all age groups studied. Growth in ponds was rapid to the time of second annulus formation, but showed a definite lag between the second and third year. In general, past the age of two years, pond bullheads had much lower growth rates than their counterparts in the other two habitats. No bullheads older than six years were taken during the study, and it is apparent from Fig. 2 that fish approaching the age of six already had begun to show unfavorable growth rates.

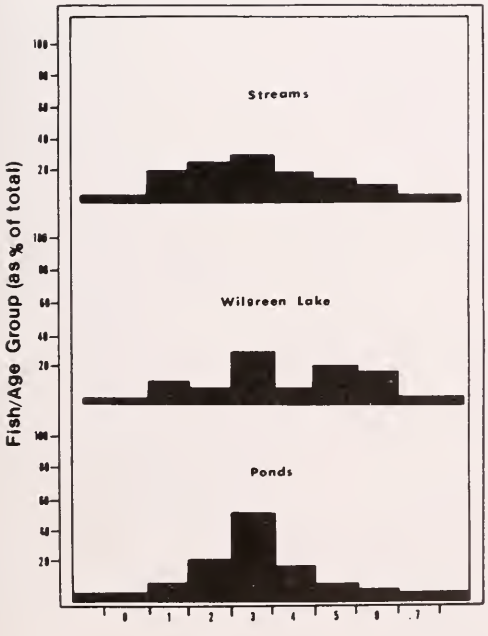

Figure 3. Age composition of pond, lake and stream populations determined from capture percentages.

Fig. 3 illustrates the population composition for the habitats sampled based on catch data. These data show definite population trends, i.e., survival through age three (the age at which most bullheads reached reproductive maturity) in ponds and streams was nearly linear, followed by an inversion of the trend after first spawnings. The polymodal nature of the Wilgreen Lake population may not represent the true population trend, but may reflect sampling bias associated with several different sampling methods, e.g., electro-fishing and trammel netting were more selective for older fish.

The populations in Ponds I and IV were subjected to mark-recovery estimations of population levels. Pond I, in conjunction with natural mortality estimates, was analyzed three times during the period October 1, 1970 to July 10, 1971. Pond IV was estimated only once, prior to the 1971 spawning season.

Pond I represented the special situation in which no fishing mortality (p) occurred during the period of investigation, but samples of the population were removed periodically. With certain carefully chosen assumptions, this situation was made to fit the Model II-B analysis of Regier (1962). The model was derived from the fact that mortality rates are either zero, infinite or directly proportional to the number of individuals in the population. Since the natural mortality (q) was assumed finite and constant, and the fishing mortality (sampling mortality in this case) was measurable over short periods of time, (q) was derivable through step-wise interation. An estimate of the natural mortality was obtained by partitioning population extremes about the calculated population line, and drawing from that line the tangent to a horizontal axis. Then, $q = -2.303\ c \tan O$, where c was a correction factor between the calculated slope b' and

the true slope be determined from linear measure of the unit cycle on the semi-logarithmic plot (Fig. 4).

The natural mortality coefficient, calculated according to the graphic method illustrated in Fig. 4, and the relationship q = −2.303 c tan O was 0.89. Extrapolated along the line $t_0 + 1$, the population curve extends for a period of one year. Thus the coefficient 0.89 represented the probability that any fish in the population would die at any designated instant in time throughout the year. Observations carried out at Pond I indicated that black bullheads were more vulnerable during spring and early summer than during other seasons of the year. Population estimates determined on October 1, 1970 (680 individuals; 413 fish per ha) and April 15, 1971 (561 individuals; 341 fish per ha) suggested that the population remained relatively stable during winter months. During the week of 13 May 1971 a mass mortality occurred in this pond, which claimed an estimated 200 fish, or 35 per cent of the original population. A similar and coincident die-off occurred in Pond V. This mortality occurred after the calculations discussed above were performed.

Reproductive Development

The reproductive development curve for pond bullheads was examined during the 1970-71 season. Fig. 5 depicts the gonad development sequence, where points are plotted as gonad weight-body weight ratios. Although the sequence of development was not followed throughout the season for lake and stream populations, spring and summer ratios for these populations are superimposed on pond curves in Fig. 5. Five stages were apparent in the development of pond bullheads. Table 5 presents delimitation of each stage, accompanied by its significance and gross morphological appearance.

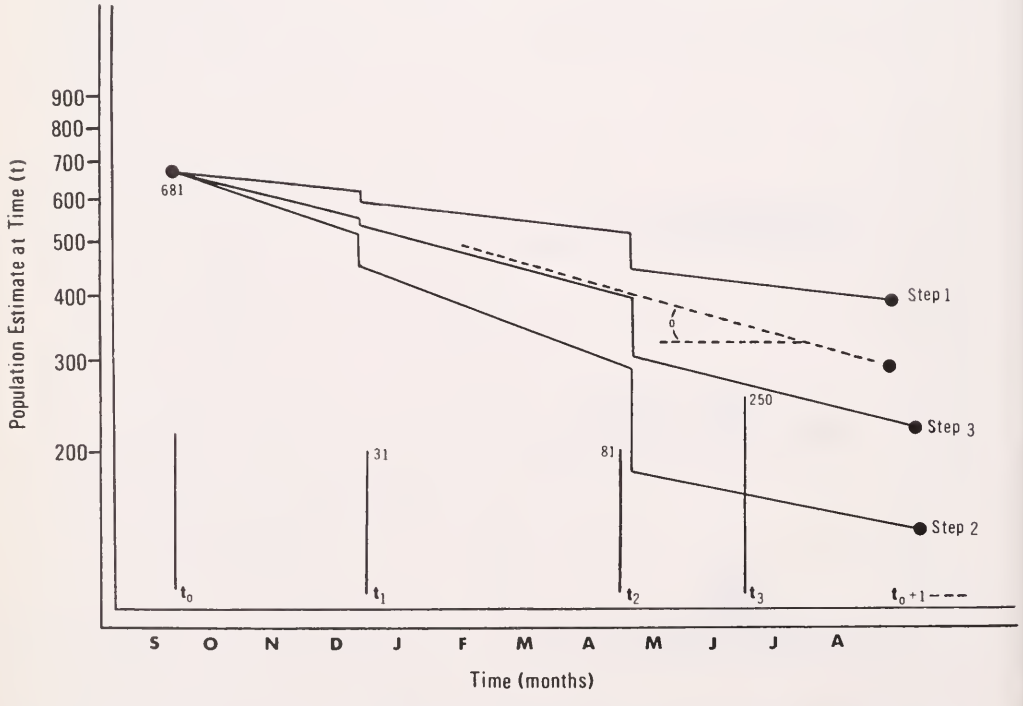

Figure 4. Graphic illustration for determination of the natural mortality coefficient (Q) by the method of stepwise iteration about the true population line.

The gonads of both males and females were at their lowest point during the post-spawning period; however, this period was apparently relatively short. Males taken during late August and early September had gonad/body weight ratios that averaged 0.7 per cent, as opposed to 1.2% for mid-August males. Female ratios varied more than those of males, but showed a corresponding increase (5.8 to 6.2%). The weight ratios of both sexes decreased sharply between September 15 and October 15, and remained low (0.3 to 0.4 for males and approximately 5.2 for females) throughout the winter. Gonad development in the spring was not an instantaneously initiated response. Although the reflex, once triggered, appears to have been irreversible, there was considerable fluctuation in the mean response with time, seemingly related to fluctuating temperatures.

Mature females reached their peak gonad development (12.1%) on 23 June, and remained relatively high until sampling was terminated on 10 July 1971. The 1970 indices remained high (10.0 to 11.5%) until mid-July. Mature males appeared to reach a reproductive peak later than females. An

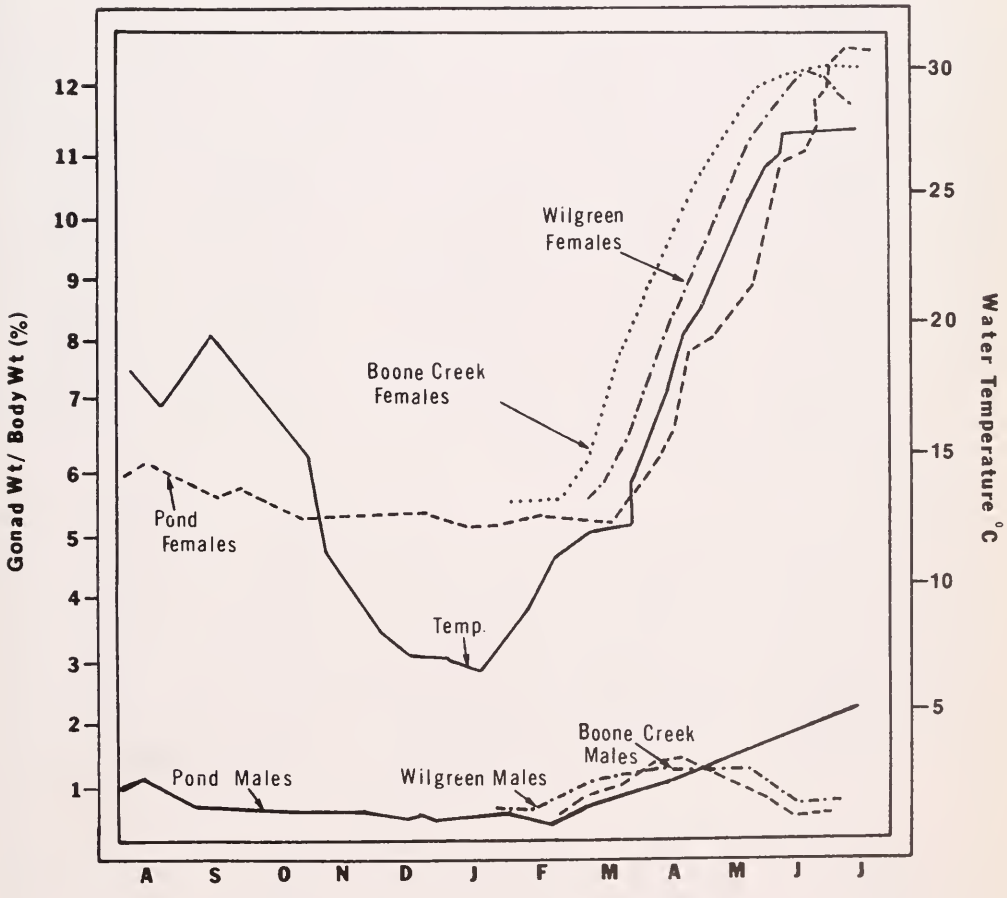

Figure 5. Gonad development curves for black bullheads obtained from ponds for the 1970-71 cycle. Imposed on the curves are corresponding records for Wilgreen Lake and Boone Creek obtained during spring and summer 1971. See Table 2 for temperature measurements.

Table 5. Appearance and significance of each stage in the gonadal development of black bullheads from pond populations.

Stage of Development	Appearance of Gonad		Significance of Stage	Period of Stage
	Male	Female		
(1)	Ribbonlike; 0.3 to 0.5 mm; extremely fimbriate margins; creamy white.	Elongate; opaque; contains primordial germ tissue and limited fat; poorly vascularized.	Quiescent stage; fat previously mobilized decreases as stage progresses. Gonad containing only primordial germ tissue.	Sept.-Feb.
(2) Developing Stage	Ribbonlike; with fimbriae increasing in dimension; pink color resulting from increased vascularization.	Oblong; eggs apparent, adhering to ovary wall; vascular areas give ovarian wall translucent appearance.	Represents initial maturation and appearance of sex products.	March-May
(3) Spawning Condition	Ribbonlike appearance lost; gonad 0.5 mm wide, 0.25 mm thick; pinkish white due to increased vascularization.	Eggs 0.5 mm in diam.; yolk fully developed and eggs free from ovarian wall; wall richly vascularized; profuse yellow color.	Sex products free in gonad (females). Both sexes ready to release sex products.	June 23 - July 1 (Females) July 1 August 1 (Males)
(4) Spent	Gonad ribbonlike as in Stage (1); uniform gray-white appearance.	Gonad flaccid; vascularization diminished to stage (2) condition; ovary wall transparent with numerous undeveloped germ cells adhering.	Sex products liberated.	Early to mid-August
(5) Recovery	Ribbonlike; gonad takes on appearance of stage (2)	Adhering germ cells fully resorbed; fatty during winter material remobilizing in gonad.	Recovery material used for maintenance.	September 1 to November 1.

TABLE 6. FECUNDITY OF BLACK BULLHEADS FROM PONDS, WILGREEN LAKE AND BOONE AND JOHNSON CREEKS. STANDARD ERROR IN MM: $S_{\bar{X}}$ = STANDARD ERROR OF ESTIMATED MEAN.

PONDS SL = 190(178-208)			WILGREEN LAKE SL = 198(186-220)			STREAMS SL = 182(164-200)		
N	Egg No.	$S_{\bar{X}}$	N	Egg No.	$S_{\bar{X}}$	N	Egg No.	$S_{\bar{X}}$
23	2552	163	7	3372	184	17	2645	237
$t_{(1,2)} = 3.3373/2.2829$			$t_{(1,3)} = .3212/2.1785$			$t_{(2,3)} = 2.4265/2.3101$		

average peak of 02.1% was recorded on 1 July 1971. Although no male samples were taken after 5 July 1971, results from the 1970 season suggested that males retain this condition for approximately 30 days.

Immature males and females had gonad development curves that mirrored those of adults throughout a good portion of the cycle. However, after reaching a plateau well below the levels found necessary for successful spawning, material previously mobilized in the gonads was rapidly reabsorbed. At the time of spawning immature gonads again reflected the refractory condition (Table 5).

The fecundity of 47 mature females of comparable size-ranges from pond, lake and stream populations was determined by a combination of displacement and egg-count methods. Table 6 presents the mean fecundity of comparable size-range females, standard errors of mean egg number estimate and Student "t" comparisons between each sample. Pond females had lower mean fecundity than females in either of the other two habitats. Analysis by Student "t" comparisons indicated significant difference between the mean fecundity value for Wilgreen Lake and the other two populations; however, the limited number of mature spawners analyzed from the former population could have masked the true relationship. Mean fecundity in ponds and streams was not significantly different ($P > .05$).

Attempts to determine egg and hatching mortality in the laboratory were unsuccessful. Subsequent to treatment with dried carp pituitary, females exhibited a sequence of behavioral changes that suggested reproductive readiness. These females went through stages of appeasement when confronted by a male, and two of the five remaining after the fifth injection constructed nests. However, males similarly treated with dried pituitary remained refractory even though long day photoperiods and temperature regulation were imposed.

On 4 July three of these pairs were terminated and their gonad/body weight ratios determined. One female (SL 207 mm, 245 g) had a ratio of 13.1 per cent, exceeding the upper limit for females taken from the wild. The remaining females (168 mm SL; 102.1 g and 172 mm SL; 134.2 g) had ratios of only 1.2 per cent and 3.24 per cent, respectively. Males ranging in standard length from 180 to 185 mm, and in weight from 132 to 139 g, had ratios of 1.5, 1.9 and 2.0, mirroring the reproductively mature condition seen in the wild (Fig. 5).

Physiological Ecology

Table 7 considers routine oxygen consumption rates for the first four free swimming stages of the life cycle of black bullheads acclimated at 7°, 12° and 23°C. Since postlarvae and juveniles were separated by

TABLE 7. ROUTINE OXYGEN CONSUMPTION RATES FOR STAGES POSTLARVA THROUGH AGE II AT 7°, 12° AND 23° C WITH THE CORRESPONDING Q_{10} VALUES BETWEEN ACCLIMATION TEMPERATURES.

Postlarva and Juveniles (A)			Yearlings (B)			Age Group II (C)		
Temp °C		oxygen consumed (ml O_2/hr)	Temp °C		oxygen consumed (ml O_2/hr)	Temp °C		oxygen consumed (ml O_2/hr)
(1) 23		0.28	23		0.17	23		0.09 (a)
	Q_{10}	1.78		Q_{10}	1.18		Q_{10}	0.12
(2) 12		0.15	12		0.14	12		0.11 (b)
				Q_{10}	1.01		Q_{10}	0.95
(3) 7		*	7		0.13	7		0.11 (c)

Significance tests (Student "t") by column and row:

Items indicated were significant at 5% level of confidence.

Column B	Row 1	Row 2	Row 3
1-3	A-C	B-C	B-C
	B-C		

* Not determined at this temperature

only a few days from the transformation date, their consumption rates were grouped. The values listed in Table 7 are accompanied by Q_{10} values computed between readings at the different acclimations. The lower portion of this table contains Student "t" comparisons for individual listings according to column and row.

These data appear to represent a uniform graded series of oxygen consumption for the life stages examined. Table 7 shows that significant differences occurred only between the extremes of observation, i.e., between postlarvae and Age II at 23°, yearlings and Age II at 23°C, and between yearlings at 12° and 23°C. The mean consumption rate for Age II at 23°C was lower than at the other acclimation temperatures; however, the means are not widely separated over the range tested, and there was no significant difference between any two readings in the series. The Q_{10} values computed between each pair of acclimations ranged from a high of 1.78 between larval means at 12° and 23°C, to a low of 0.12 between the means of Age II at these same acclimation temperatures.

Oxygen consumption increases in a nearly linear fashion when plotted on a double logarithmic grid (Fig. 6), where the lines are fitted by a least squares method. Such a plot, if representing a true linear relationship, presumably should show the magnitude of temperature effect on oxygen consumption by changes in the slopes of the lines for different temperatures. Fig. 6 reveals that there was less than an ideal lineation between the log of oxygen consumption (mg) and the log of weight in grams. However, since the tendency for consumption to decrease with respect to the log of weight after the first year was constant for the two temperatures, the slopes of the two regression lines were analyzed as to their homogeneity. There was no significant difference apparent between the slopes ($F_s = 1.0018/F(1, 38) = 7.35$).

Oxygen consumption rates were also

measured for fish ranging from 20.15 to 37 mm as functions of decreasing oxygen concentrations. It was found that these bullheads could extract maintenance oxygen down to 0.01 ml/hr in oxygen tensions of 0.2 to 0.5 ppm. Below these levels, asphyxiation was imminent, and the runs were terminated. Carbon dioxide tensions of 10.5 to 21.0 ppm were routinely determined by titration with 0.01N NaOH at the points of minimum maintenance.

Mean critical thermal maxima (CTMax) for the four age groups, postlarva through age II, are graphically illustrated in Fig. 7. Here also, physiological tolerance was related to stage of development. Postlarvae, acclimated to 12° and 23°C, had critical thermal maxima that increased 0.14°C per degree increase in acclimation temperature, in contrast to 0.09, 0.14 and 0.23 for juveniles, yearlings and age II, respectively, over the same range. There were significant differences in the effects of acclimation temperature on different age groups. All four groups had significantly different means at 23° and 12°C, ($P = 0.05$); however, only the age II group had a significant difference in the mean of 7° acclimation when compared to the two higher means ($P < 0.05$), although the spread may not have been adequate to demonstrate difference.

Temperature-preference ranges were determined for the first three age groups (above). Selected frequencies, along with

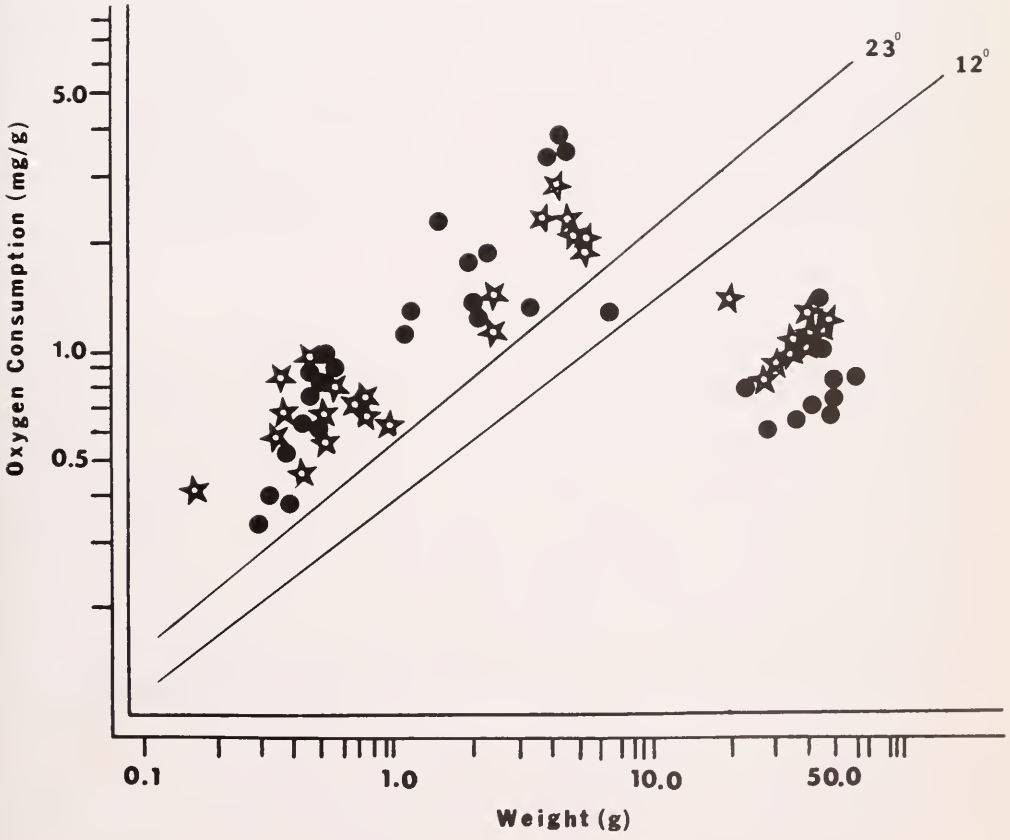

Figure 6. The influence of weight on routine oxygen consumption at 12° and 23°C. Solid circles= 23°log Y=−0.189 + 0.075 log X; open stars=12°log Y=−0.042 + 0.1124 log X.

TABLE 8. ANALYSIS OF TEMPERATURE PREFERENCE OBSERVATIONS FOR POSTLARVAL, JUVENILE AND YEARLING BLACK BULLHEADS AT 7°, 12° AND 23°C. M= MEDIAN FREQUENCY SELECTED, N= NUMBER OF ANIMALS OBSERVED, R = DURATION OF EACH OBSERVATION IN HOURS, x^2/x^2 .05 FOLLOWING EACH COLUMN COMPARES THE SELECTED FREQUENCIES OF ALL GROUPS AT THE SAME ACCLIMATED TEMPERATURE, AND x^2/x^2 .05 FOLLOWING EACH ROW COMPARES THE SELECTED FREQUENCIES OF INDIVIDUAL GROUPS AT THE THREE ACCLIMATION TEMPERATURES* . POSTLARVAE WERE NOT ACCLIMATED AT 7°C.

7°			12°			23°			
N	R	M	N	R	M	N	R	M	x^2/x^2 .05
Postlarva			Postlarvae			Postlarvae			
			10	9	25.1-27.0	10	9	23.1-25.0	17.89/3.84
Juveniles			Juveniles			Juveniles			
10	9	17.1-19.0	10	9	21.1-23.0	10	9	19.1-21.0	7.92/4.82
Yearlings			Yearlings			Yearlings			
9	9	19.1-21.0	10	9	19.1-21.0	10	9	19.1-21.0	26.02/4.82
x^2/x^2 .05		28.67/3.84			30.68/4.82			35.55/4.82	

* In order to compare the selection frequencies, the assumption was made that groups representing the same population with respect to temperature preference should have the same median frequency. After making this assumption, the frequencies were treated with the nonparametric "Median Test" of Downie and Heath (1961).

methods of comparison, are presented in Table 8. Generally, temperature preference inflected downward with progressive stage of development. In addition, acclimation to lower temperatures shifted preference temperatures upward for the first two life stages. Preference temperatures ranged from 23.5° to 27.0°C for postlarvae; 18.0° to 21.0°C for juveniles, and remained relatively unchanged with acclimation, 19.1° to 21.0°C, for yearlings. These data were gathered over nine-hour periods in continuous light. Postlarvae, brought into the laboratory from 23°C environmental temperature, showed a characteristic ascendence toward the temperature shown in Fig. 8; however, after 10 hours in the chamber these fish almost instantaneously shifted to a lower temperature (17.5° to 19.0°C). Two more sets of larvae were acquired to determined the character of this shift, and on each separate run the same phenomenon was observed.

These data, along with critical thermal maxima and lower lethal temperature points (determined as the point at which no further death occurred with time) were represented as incorporations into the over-all thermal picture. Fig. 8 displays the thermal polygons of postlarvae, juveniles and Age II. Since lower lethal temperatures were not determined for yearling bullheads, only their preference was imposed on the graph. Fig. 8 shows that each stage had a distinctly different temperature polygon. Postlarvae had the highest upper mean limits, but this increase was compensated by the upward inflection of lower limits. Larvae measured at 23° had a lower lethal temperature of 9°C, and at 12°C acclimation, a lower limit of 7°C. Juveniles acclimated at the same temperatures had lower lethal limits at 2.5° and 4.0°C, and Age II individuals had limits of

0.5° and 1.0° at 12° and 23°C, respectively. The two latter groups, when acclimated at 7°C, had lower lethal temperatures corresponding to the freezing point of water. Preliminary analysis suggested that the true lower limit was probably more closely related to the supercooling capacity of the water. Samples of blood serum, washed with heparin, centrifuged and suspended with equal volumes of water in an ethylene glycol bath suggested that serum had a freezing point of 0.8°C lower than the freezing point of water. However, this investigation was too limited to merit consideration here.

DISCUSSION

Population Dynamics

There has been disagreement in the few past studies that have sought to determine black bullhead feeding habits, although the differences may be more apparent than real since the individual authors used different terminology and were not principally interested in electivity and the relative abundance of food. Several authors (Trautman, 1957; Clay, 1962; Smith, 1949) assessed the feeding habits of this species as truly omnivorous. Forney (1955) and Viosca (1931) suggested that feeding probably was selective, since great numbers of chironomids were consumed. Rose and Moen (1951), on the other hand, contended that this tendency to rely on chironomids simply reflected the preponderance of this item in the food supply. Kutkuhn (1955) listed a variety of food items taken by adults; however, no single item was assumed to predominate in the food consumed. None of these investigations employed selective feeding analysis.

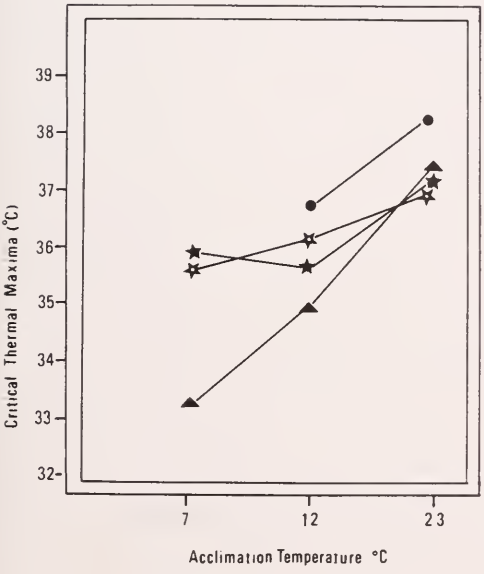

Figure 7. Mean CTMax values for stages post-larva through age II at 7°, 12° and 23°C. Post larvae were not acclimated at 7°C; consequently, only the means obtained at the other acclimation temperatures are included. Solid circles=post larvae; open stars=juveniles; solid stars=yearlings; solid triangles=age group II.

Our study clearly demonstrated that certain foods were selected for, and others against, and that although chironomid larvae and pupae did make up a sizeable percentage of the total complement (39.0 to 55.0%) in lake, pond and stream habitats, their selectivity ratio was no greater than less abundant foods (Table 3).

A notable percentage of specimens captured prior to the spawning season 1971 had eaten measurable quantities of filamentous algae and plant debris. Forney (1955) indicated that there was a necessity for this species to feed on plant material in order to reach reproductive readiness, and Raney and Webster (1940) noted a sequence of feeding in early spring which included several plant foods. We could not substantiate the former contention during this study. One of the ponds most heavily sampled during the survey contained no plant material except members of the Cyanophyta, yet the bullheads in this pond reached reproductive readiness, as expected, during the 1969-70 and 1970-71 seasons. Feeding intensity, but not pattern, changed markedly throughout the year.

Stream populations took a greater variety of food items than did individuals in either of the other two habitats. Possibly this resulted from greater availability rather than enhanced selection.

Larval feeding appeared to be even more selective than that of adults. Larvae and

juveniles relied heavily on the aquatic amphipod *Hyalella,* ostracods and adult copepods, but selected strongly against the nauplius larva of the latter and the truly benthic components relied on most heavily by adults. This was essentially the same food consumption described by Ewers (1931) and Forney (1955). However, the former authors concluded that peaks of feeding activity occurred just before dawn. Early morning samples taken during this survey indicated that relatively less feeding occurs during early morning than during mid-day. With respect to food selection, no other studies have indicated preferences as functions of available items. We concluded that items were selected for, not according to their availability, but according to the position and abundance they assume in the habitat.

Observation of larval feeding suggested that it occurred along a visually or otherwise determined orientation axis. Since it is well documented that young bullheads have poor visual acuity, and correspondingly advanced chemical perception (Bowen, 1931), orientation is believed to result from a combination of sensory mechanisms. However, orientating larvae appeared to establish an axis of the Y-axis type described by Ferguson, Landreth and Turnipseed (1965). Disturbed larvae tended always to reaggregate toward this imagined line which formed perpendicular to the shoreline. Feeding also appeared to be restricted to a rather limited locus about this same axis of orientation, with the bulk of feeding occurring during daylight hours.

Ponderal indices measured during April, May and June 1971 for specimens from pond, lake and stream populations were highly comparable from one habitat to another ($P = 0.05$). Since these ratios, reported throughout the range, are quite variable from one state to the next, there seems little value in making such comparisons here (see Carlander, 1968). Comparability from one habitat to another is, however, important. Length-weight regressions for the same populations were found to be heterogeneously distributed, as indicated by analysis of their slopes ($F_S = 29.69/F(2, 103 = 4.82)$. In addition, length-weight correlations for the three populations were quite variable, the highest values obtaining in Wilgreen Lake ($r = 0.68$). It was difficult to attach significance to this finding since variance between the separate populations could lead to lower values. Investigators in other parts of the black bullhead's range have reported both high and low length-weight relationships (Dennison, 1970; Lewis, 1949; Carlander, 1968). Our findings did serve to point out that members of the single species tend to show deviate population trends when encountered in different habitats.

The size in length and weight at the time of annulus formations were compared. Generally, increase in length was more closely related to age than increase in weight (Fig. 2). The size at the time of each annulus formation showed greater mean differences in ponds where there was a growth lag between the second and third year. This finding is in line with the conclusion drawn by Houser and Collins (1962), who found that growth rates in Oklahoma bullhead populations were lowest in ponds. It also appears to augment the observations of Moen (1959) that black bullhead growth is retarded according to the degree of intraspecific competition, which is doubtlessly more influential in ponds than in streams. Three of the ponds utilized during this study, Ponds I, IV and V, were overcrowded with bullheads. A fourth pond, Pond II, was overpopulated by the bluegill sunfish. However, the effect of overcrowding by this second species was not reflected in bullhead condition. Population estimates in Pond I indicated the conditional and genetic effects of crowding. On October 1, the population of this pond was estimated at 681 fish, or 1,021 fish per surface acre of water (431/ha). Hastings and Cross (1962) and Fredin (1950) reported the presence of similar sized populations in turbid ponds, and commented on the relationship of crowding to weight gain. The age-weight correlation determined for ponds during this study (heavily weighted by crowded pond specimens) was quite low ($r = 0.42$).

A great number of abnormalities were observed in the Pond I population, apparent-

ly resulting from overcrowding. Several fish were captured which lacked one or more fins, and one individual captured during July 1971 had no paired fins at all. In addition to abnormal fish, most of the breeding population in this pond suffered from bacterial fin rot during spring and early summer. Microscopic examination revealed the presence of a proliferative streptococcus bacterium.

Apparently, then, from samplings of three different populations within a comparable area, the greatest population success is probably achieved in ponds, as indicated previously by Houser and Collins (1962). However, this does not imply that greatest population survival also occurs in ponds. From observations during the period September 1, 1970 to July 10, 1971 a natural mortality

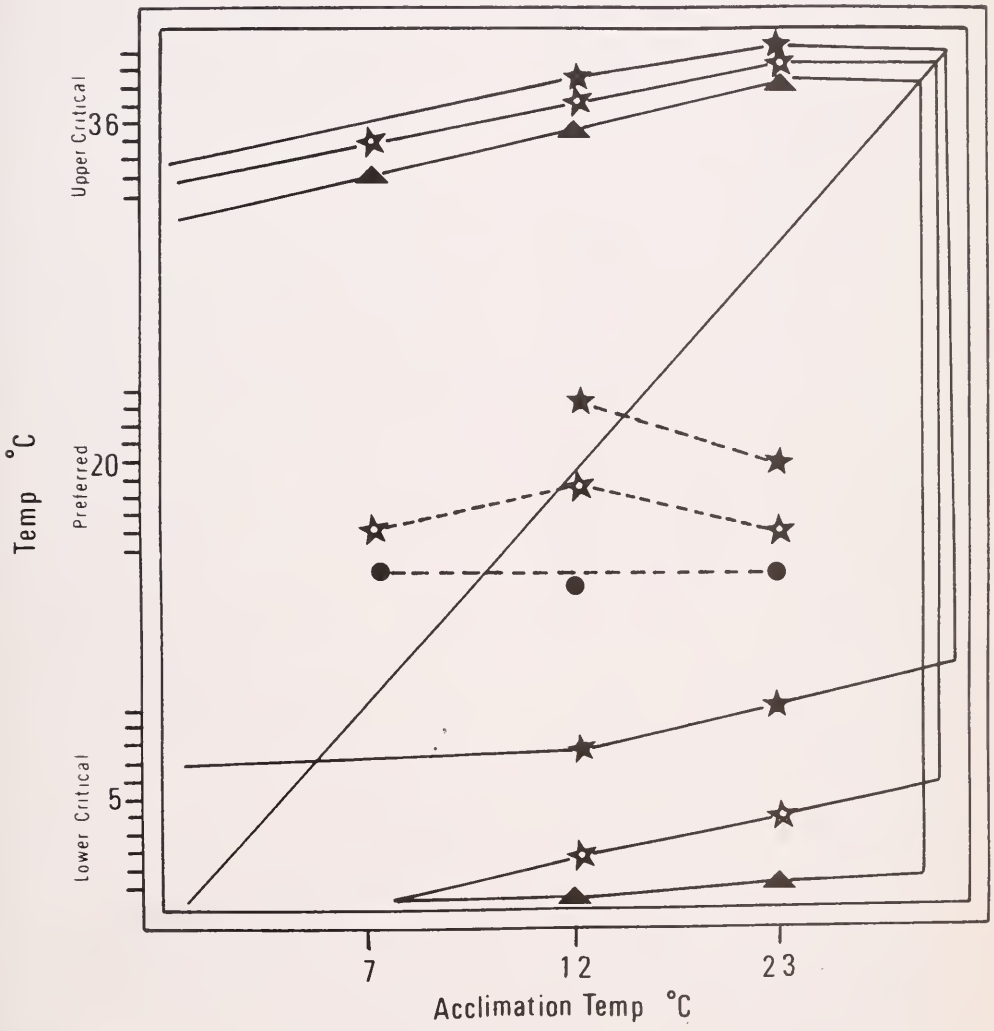

Figure 8. Relation between mean upper and lower lethal temperature limits expressed as functions of acclimation temperature for stages postlarva, juvenile and age II. Included are the preferred temperatures of postlarvae, juveniles and yearlings similarly expressed as functions of prior acclimation. Solid stars= postlarvae; open stars=juveniles; solid circles=yearlings; solid triangles=age group II.

coefficient was computed for the population of Pond I. The result suggested that each adult fish in the population had only an 11 per cent chance for survival throughout the year. Apparently, there are no natural mortality estimates available with which to compare this one. Taken as an absolute value, however, it does indicate that mortality was high for the period of one year. However, further estimates of population sizes suggested that mortality was neither infinite, nor evenly distributed throughout the year. A population estimate made during the week of 15 April 1971 disclosed the presence of 562 bullheads, 83% of the original estimate that had survived through the winter. Thus, heavy mortality did not occur during winter months. This seems to augment the contention of Forbes and Richardson (1908) that black bullheads enter a relatively quiescent state during periods of prolonged cold. Nordlie (1966) further noted that peptic digestive rates could be directly related to temperature regimens, increasing or decreasing with temperature over relatively short periods of time. Fish were captured throughout the winter, and on one occasion the ice was broken in order to remove traps containing bullheads. These fish had no food in their stomachs, but were active enough to enter traps. Thus, although retaining some active impulses, winter bullheads appeared to survive reasonably well without food by the conformity of certain physiological mechanisms to reduced temperatures.

During the second week in May 1971 a naturally occurring mass-mortality was observed in Ponds I and V. This occurred during a period of heavy rainfall and unseasonally cool weather, and the water temperature in Pond I was reduced 7.0°C. Although the overall water chemistry picture did not change appreciably, the dissolved CO_2 concentration increased from 4.5 to 14.0 ppm over a two-day period (Table 2). An estimated 200 fish died in Pond I, 29% of the original population estimate. The bulk of the mortalities were older fish, and mature individuals approaching the breeding condition. Powers (1937) commented on similar mortalities and implicated CO_2 changes as the most instrumental factor in mortality. This contention, however, could not be substantiated during our investigation.

Black bullheads older than six years were not taken during this study. This seemed to indicate that the longevity for members of the species was relatively short, and in Fig. 2 one sees that bullheads approaching the age of six had already begun to show unfavorable incremental growth. Rose and Moen (1951) followed a single black bullhead year class through 10 consecutive years in Lost Island Lake, Iowa. Few individuals survived past the age of seven, and those that did remain showed unfavorable growth rates.

Reproductive Potential

As noted in Table 5, material began mobilizing in the gonads of pond bullheads shortly after the spawning season; however, most of this extragonadal tissue had been reabsorbed before temperature increases in spring initiated the developmental stage. From the quiescent stage brought on by cold it could be surmised that this same sequence should prevail in all populations. However, stream bullheads spawned at least one month previous to the other populations, with peak gonad/body weight ratios attaining during early and mid-May (Fig. 5). Two apparent explanations might account for this difference in spawning time and developmental sequence: (1) although constant rise in temperature appeared to initiate the reflex in ponds (Fig. 5), and in lakes (Dennison, 1970), a separate and distinct set of conditions might prevail to initiate the spawning response in streams; (2) as Aronson (1955) disclosed for the cichlid *Tilapia heudiloti*, which spawns throughout the year but has spawning peaks corresponding to the vernal and autumnal equinox, each individual may have a temperature threshold distinct from others in the populations, producing noticeable differences when different habitats are considered.

Pond and lake spawners also react differently to temperature. Dennison (1970) indicated that once initiated the response in Clear Lake, Iowa, was nearly linear and un-

interrupted. In both situations, once initiated, the developmental sequence appeared to be irreversible. In Wilgreen Lake, where temperature fluctuations were not marked over short periods of time, the gonad/body weight curves showed interrrupted increases. In contrast, corresponding ratios for pond spawners fluctuated directly with temperature change (see Table 2). This probably was a parametric manifestation of the alternate speeding-up and slowing-down of physiological rate functions in response to rather widely fluctuating temperatures (Table 2). Regardless of the influence, pond spawning lagged behind that of Wilgreen Lake, with pond males and females reaching the most favorable gonad/body weight ratios (2.1 and 12.1%) on July 3 and June 23, respectively.

The above comparison shows that the habitat imposed its own limit on breeding time and the sequence of reproductive development. Thus, it is not difficult to reckon if one considers that different bodies of water mediate environmental modifiers differently and prompt the establishment of genetic stocks that adjust the breeding sequence to the most favorable period of the year.

Fecundity determined during this study also showed considerable variability when all three habitats were considered. Greatest mean fecundity per individual attained in Wilgreen Lake (mean = 3,372), with ponds exhibiting the lowest value (mean = 2,552), and streams intermediate (mean = 2,645) (Table 6). Mean values between the lake and other populations were significantly different at the 5% level of confidence.

Few fecundity estimates have been published for black bullhead populations and the reports that have appeared have represented lake populations. Thus, the data obtained during this study probably are more significant when the different habitats are compared. Pond fecundity apparently is reduced coincident with the limits of intraspecific competition, similar to the situation that accrues with growth (Moen, 1959). This assumption is difficult to make for streams which had equally low mean fecundity. Data for Johnson and Boone creeks were combined to arrive at the value listed in Table 6; however, from individual estimates made in Boone Creek during the 1969-70 season (7 specimens) we assumed that all overall fecundity was greater for this stream (mean = 3,845) than for the other. Johnson Creek presented a situation similar to that observed in ponds. The water was turbid during the period of sampling, and on a single night of seining over 500 bullheads were hauled from a .20 km section. Therefore, overpopulation here seems to have had an effect on mean fecundity similar to that recognized in turbid ponds.

Attempts to induce spawning in black bullheads proved unsuccessful. There has been considerable controversy over methodology when employing pituitaries to induce spawning. Early investigators (Hasler, Meyer, and Field, 1939; Pickford and Atz, 1957) insisted that only fresh preparations should be used. Indian biologists, however, have achieved considerable success with dried pituitary preparations administered through intramuscular injection (Alikuhni, Sukumaran and Parameswaran, 1962; Alikhuni and Sukumaran, 1962). The Indians indicated that great numbers of the silver carp *(Hypothalmichthys molitrix)* had to be obtained to acquire a relatively few fish that could be artificially stimulated. Others (Sneed and Clemens, 1960) preferred the intraperitoneal route of injection, but concluded that greater dosage rates are required.

Wallace (1967) used the methods detailed by Sneed and Clemens *(loc. cit.)* and was successful in inducing black bullheads to spawn; however, his results were based on the observation of a single breeding pair retained in a 400 gallon (1514 l) gallon aquarium from the end of one spawning period to the beginning of the next. Perhaps in contrast to the refractory nature of spawners held in aquaria during this study, that a pair of fish kept over an extended period may retain an endogenously controlled reproductive rhythm, such as that described for certain small mammals and birds (Pengelley and Asmundson, 1971). If so, such fish could conceivably spawn naturally.

The method used during the present study followed that of Sneed and Clemens

(loc. cit.) and Wallace *(loc. cit.)*. This method, which suggests the administration of 4 mg/lb (1.82 mg/kg) per day of dried pituitary, was devised for channel catfish, the authors suggesting that breeders should be obtained as close to the spawning season as possible. Other authors (Pickford and Atz, 1957) suggested different stages of reproductive readiness during which riverine fishes should be obtained in order to obtain the best results. Although our experimental fishes oozed gametes when strong pressure was applied to the abdomen, they did not respond to pituitary treatment. We have no explanation for the failure of black bullheads to spawn in aquaria. When our experiments were terminated on July 5, the catfish exhibited gonad/body weight ratios similar to those observed in the wild. This would seem to indicate that the attainment of reproductive readiness was not the chief limiting factor.

Physiological Ecology

Several investigators have commented on the black bullhead's ability to persist in situations that are limiting to most other fishes (Black, 1955, 1959; Lewis, 1949,; Trautman, 1957; Bennett, 1948), because of combined behavioral and physiological adaptations which enhance the ability of rate functions to remain relatively constant over a wide spectrum of environmental gradients. However, information is conspicuously meager in the area of black bullhead physiological ecology. Temperature thresholds and oxygen consumption rates have been determined in the brown (Brett, 1944) and the yellow bullheads (Morris, 1965), but only incidental treatments have been reported for the black bullhead. As indicated by Brett (1971), temperature is probably the most important controlling factor in distribution and life styles of most fish species. For this reason, tolerance points relative to different acclimation temperatures must be established, and extrapolated from them to obtain the thermal survival picture. However, Brett (1959) and Hart (1952) questioned the imposition of temperature tolerance points that fail to reflect environmental survival, i.e., the physiological and ecological limits are often widely separated. Furthermore, fishes rarely live in conditions close to their survival thresholds.

In general, temperature tolerance polygons occur as a graded series when more than one stage in the life cycle is considered (Fig. 8). Extremely high upper limits (39°C for postlarvae acclimated at 23°C), and lower limits restricted to a narrow range about the freezing point of water for older animals, assure this species a position in most habitats. We observed as well that the critical thermal maxima curves for four different life stages were also graded, each stage exhibiting a relatively flattened curve with respect to closely related species (Brett, 1956). The oldest group tested (age II), and two intermediate stages, exhibited relatively good compensatory ability with respect to temperature change; whereas postlarvae at the two acclimations 12° and 23°C showed less ability to compensate for temperature change through alteration in rate functions. Since the postlarval stage could not be acclimated to 7°C, we suggest that black bullheads are not hatched with the ability to compensate for wide change in temperature. However, since they are born during a period of the year when environmental temperatures are highest, the tolerance to high temperatures (Fig. 7) probably is most important. As indicated by the curve for juveniles (Fig. 7), after attaining a few days of age (10 to 15 days) the biochemical structure is sufficiently enhanced to permit compensations over a wider temperature range.

Brett (1956) constructed thermal polygons similar to the ones we depict in Fig. 8 for the brown bullhead. The black bullhead, as determined by us, appears to have a greater tolerance range at comparable acclimation temperatures.

Hart *(loc. cit.)* and Brett (1959) concluded that temperature tolerance is not of direct ecological significance, since fishes rarely confront such temperatures. However, our work indicates that black bullheads can or do live close to their thermal limits during at least a portion of summer and early fall. The temperature of Ponds III and IV reached 33°C even in the deepest parts on

several days during August and September. Even if temperature tolerance fails to reflect a true ecological condition, it does indicate the ability of a species to alter rate functions in connection with temperature changes, which suggests that such species function effectively over very broad thermal zones.

The temperature preferences of three age groups of black bullheads were investigated (Fig. 1). Different stages in the life cycle were found to have significantly different preference ranges over the acclimations indicated above ($P < .05$, Table 8). In addition, a phenomenon was observed in larvae which suggested the influence of temperature on life style at this stage. Postlarval bullheads held in the selection chamber for nine-hour periods behaved much like older fish. However, after ten hours in the chamber, they suddenly shifted from one preferred temperature to a lower one (from 23.5° to 17.5-19°C at 23°C acclimation). After subsequent experimental runs demonstrated the same response, we theorized that this was an environmental artifact, i.e., that larvae apparently had free running rhythms of activity. After spending daylight hours near the water surface they sought lower strata of water where seclusion was more nearly assured. We suspect that the response observed in the chamber was the same as that which occurred in the wild. Larvae apparently sought water in which to remain secluded by seeking water temperatures associated with that stratum. The reciprocal explanation could also be advanced according to the time of day.

Three levels of oxygen consumption have been described for fish: standard, routine, and active (Fry, 1968). Routine rates, which may be defined as the oxygen consumed by a fish whose only movements are spontaneous (Beamish and Mookerjii, 1964). Such readings are most frequently recorded, and their values fall between the extremes of active and standard metabolism. The rates of oxygen consumption at different acclimation temperatures are still another, and perhaps better, indicator of change in rate-function with time.

Morris (1965) stated that brown bullheads, when moved to 27° from 12°C acclimation, compensated by lowering metabolic levels from 0.35 to 0.15 ml O_2/g/hr. The routine rates measured during the present study indicated that black bullheads do not display such compensatory shifts over a 16°C change in temperature. However, since their rates were significantly low even at the highest acclimation temperature (Table 7), and since all rates were measured at 20°C, such radical compensatory shifts were not anticipated. We believe that the black bullhead is able to survive in extremes of temperature by having a relatively flattened metabolic rate curve, which hardly doubles for each 18°F increase in temperature as indicated by McCay (1925).

Beamish and Mookerjii (1964) and Basu (1959) suggested that oxygen consumption increased linearly with weight when plotted on a double logarithmic grid. This appeared to hold for our first two groups (Table 5) but not for age II individuals, whose absolute consumption fell below the best fit line (Fig. 6). However, since we assumed that the effect was constant from one acclimation temperature to another, the only factor operating to account for changes in consumption is temperature. From an analysis of the homogeneity of the slopes plotted for 12° and 23°C acclimation, we determined that there is no significant change in routine consumption for an eleven degree change in temperature ($F_S = 1.0018/F.99\ (1, 38) = 7.35$).

According to Prosser and Brown (1962) chemical reaction rates usually are more than doubled for each 10°C increase in temperature. Thus, Q_{10} values of less than 2 would indicate a relatively insensitivity to temperature. The Q_{10} values determined for black bullheads (Table 7) ranged from 1.78 for postlarvae to a low of 0.12 for age group II.

The most important observation drawn from metabolic-rate determinations was the fact that black bullhead rates decreased to a maintenance level of 0.01 ml O_2/g/hr at 0.2 to 0.5 ppm dissolved oxygen before showing signs of asphyxial stress. However, this should not be considered unique. Larimore

(1957) reported similar low levels for the warmouth, *Chaenobryttus gulosus,* and Powers (1938) found that other fishes, such as the smallmouth bass, *Micropterus dolomieui,* could extract oxygen to 0.3 - 0.4 ml/l. We doubt, however, that this fish could have established maintenance levels as low as that determined for the black bullhead.

The black bullhead is known to survive in habitats that present far less than the ideal conditions of temperature and dissolved oxygen. Presumably this is possible through a combination of ecological and physiological adaptations. The ability to subsist on a variety of foods, or on a very limited food supply, and the ability to become quiescent during periods of prolonged temperature decrease are significant adaptations to life in some of the habitats occupied. In addition, comparatively favorable high and low lethal temperature ranges, assure the species a position in most situations that might prove limiting to less favored species. Low metabolic rate-temperature curves imply at least one rate function that changes minimally with temperature, and the ability to extract maintenance oxygen in the presence of low ambient levels favor survival in most extreme situations.

SUMMARY AND CONCLUSIONS

Although the black bullhead is widely distributed in the United States it has not been studied extensively. Our study was designed to facilitate a better understanding of the species' life history and physiological responses in pond populations, as compared to other known habitats. Conclusions from data derived during April 1970 through July 1971 are summarized as follows:

1. Adult black bullheads subsist on a variety of foods, but exhibit feeding selectivity in ponds, lakes and streams. Chironomid larvae, comprising a predominant portion of the adult diet, are not more strongly selected for than other less available foods.
2. Larval feeding occurs in a rather restricted locus about an axis of visual orientation. Foods taken most frequently by young are the aquatic amphipod *Hyalella,* ostracods and adult copepods. Larval feeding was found to be highly selective.
3. Mean ponderal indices for pond, lake and stream populations do not differ significantly ($P < .05$). However, log-transformations of length-weight relationships have slopes for which the hypothesis $B = 0$ does not hold at the 99% level of confidence. Most favorable growth rates occurred in Wilgreen Lake, and least favorable in ponds. The age-weight correlation for pond populations was quite low ($r = 0.42$).
4. Populations attained high levels in ponds [1,021 fish per surface acre (= 413/ha) in one 0.65 (= .26 ha) acre = impoundment]. The effect of crowding was significantly reflected in population condition, number of genetic abnormalities and lowered mean fecundity. Also apparently correlated with high population levels was a high mortality coefficient (0.89 for Pond I of this study).
5. Mortality is appreciably higher during some portions of the year than others. Greatest mortality occurred in Pond I during spring and early summer. Population estimates indicate that mortality is relatively low during the winter.
6. Gonadal development and attainment of spawning condition in ponds lag behind that of lakes and streams. Most favorable gonad/body weight ratios occur in June for mature females (12.1 per cent) and July for mature males (0.21 per cent). In contrast, stream spawners reach development peaks during mid-May, and Wilgreen Lake spawners attain the most favorable index during mid-June.
7. Fecundity for females ranging from 164 to 220 mm SL is lowest in ponds (mean - 2,552), highest in Wilgreen Lake (mean = 3,372) and intermediate for combined samples from creeks (mean = 2,645).

8. Mature bullheads brought into the laboratory during the month of May could not be induced to spawn even after repeated treatment with dried carp pituitary gland. The gonad/body weight ratios of these fish on the termination date, 5 July, were similar to levels observed in wild populations.
9. Temperature tolerances were sufficiently high and low that few habitats could be considered restrictive to bullhead survival on the basis of temperature alone. The CTMax of age groups postlarva through Age II ranged from 36.5° to 38.2° at 23°C acclimation. CTMax curves over a temperature range of 16°C were relatively flattened, suggesting little rate-function change with temperature. Lower lethal temperature graduated upward for each descending stage of the life cycle. Preference ranges for the first three life stages were significantly different from one another at the 5% level of confidence.
10. Metabolic rate-temperatures curves, Q_{10} values, and absolute consumption at different temperatures suggest that metabolic rates change very little over a 16°C acclimation range. Black bullheads of 20.15 to 37.00 g reached the maintenance oxygen level at 0.1 ml O_2/g/hr in 0.2 to 0.5 ppm ambient oxygen.

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NOTES ON THE BREEDING BEHAVIOR, EMBRYOLOGY AND LARVAL DEVELOPMENT OF *CYPRINODON VARIEGATUS* LACÉPÈDE IN AQUARIA[1]

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ABSTRACT

Several adult *Cyprinodon variegatus* were placed in aquaria, maintained at 23°C, where reproductive behavior was observed. After each spawning the eggs were collected and observed to record the developmental stages. They were 1.4 - 1.6 mm in diameter, spherical, and covered with semi-adhesive threads. Embryological development proceeded rapidly at first but slowed in the later stages. Hatching was first observed between 120-125 hours after fertilization. Newly hatched prolarvae were 3.0 mm in total length, had 24 myomeres, black eyes and an apparently fully developed mouth. The heart was visible and the heart rate averaged 124 beats per minute. A fin fold was present that contained seven or eight caudal but no dorsal or anal fin primordia. One or two fin ray primordia were present in each pectoral fin. The vertical fins were developed and the fin fold had disappeared on individuals over 8.2 mm standard length. Pelvic fin buds began to develop last (at about 8.1 mm SL) and all rays were present at SL 9.0 mm. All individuals possessed most adult characteristics at 12-13 mm SL.

INTRODUCTION

Various aspects of the early life history of *Cyprinodon variegatus* have been reported by several investigators; however, none have given a complete description of the sequence of events beginning with the spawning behavior and extending to the development of juvenile individuals. Newman (1907) presented the first data on the spawning activities of *Cyprinodon variegatus* in aquaria. His observations were later supplemented by Raney, et al. (1953) based on observations in south Florida lagoons. Kuntz (1916) gave the most complete account of the embryology of the *Cyprinodon variegatus* but emphasized information that would aid in the ready identification of the eggs and larvae rather than details of its embryology and development. Hildebrand (1917), Hildebrand and Schroeder (1928), Nichols and Breder (1927) and Simpson and Gunter (1956) reported on various aspects concerning the life history of *C. variegatus* along the Atlantic and Gulf coasts. Most of these data were summarized by Breder and Rosen (1966). The two most recent comprehensive studies on estuarine larval fishes are those by Lippson and Moran (1974) and Scotten, et al. in 1973. The data presented on *C. variegatus* in those reports, however, is essentially a summary of earlier studies.

The purpose of this report is to give a complete account of the reproductive sequence of *Cyprinodon variegatus* including spawning behavior, embryology and larval development. Where possible, our observations and results are compared with those of earlier studies.

MATERIALS AND METHODS

Specimens of *Cyprinodon variegatus* were collected from a tide pool to Mobile Bay, Mobile County, Alabama on 7 April 1974. They were placed in a styrofoam container and transported to the laboratory at the University of Alabama and several males and females were placed in each of two 40-L aquaria filled with freshwater and a clean sandy substrate. Water temperature was

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maintained at 23°C ±1°. Fishes were fed brine shrimp *(Artemia)* nauplii each day. The room that housed the aquaria was maintained on a 14-hour light/10-hour dark photoperiod using banks of fluorescent lights controlled by an automatic timer. This lighting was augmented with daylight.

After each observed spawning, the eggs were removed from the aquarium and placed in small culture dishes. Eggs obtained from unobserved spawns were sorted into separate dishes based on their stage of embryonic development. In the initial stages of the study, observations on eggs were made continuously in order to record all embryological changes, however, after the development of several groups had been thoroughly monitored and a schedule of the principal embryonic stages had been devised, eggs were checked only periodically. A written and photographic record of the developmental process was kept throughout the study. Terminology employed in the descriptions of eggs, embryological stages and larvae is similar to that used by Hubbs (1943), Rugh (1962), and Blaxter (1969). Eggs were photographed with a 35 mm single lens reflex camera through a dissection microscope using tungsten light.

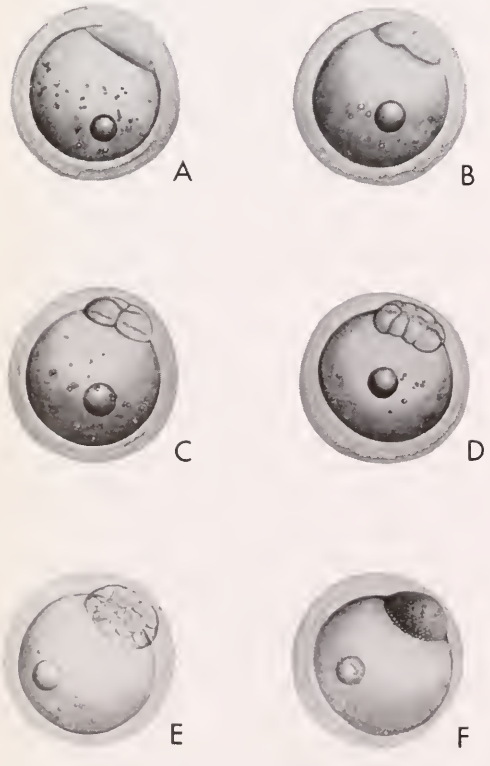

Figure 1. Developing eggs of *Cyprinodon variegatus*. A. One-celled stage; B. Two-celled stage; C. Four-celled stage; D. Eight-celled stage; E. Early blastula; F. Late blastula.

On about the third day after hatching, the prolarvae were fed freshly hatched brine shrimp *(Artemia)* nauplii. This food supply was maintained throughout the study. After each feeding period, uneaten nauplii were removed from the culture dishes to avoid problems of fungus growth associated with water spoilage and disease.

During the period after hatching, one or more individuals were periodically preserved in a 5% formalin solution for observation and measurement. The schedule for preservation of specimens was irregular and dependent on the amount of morphological change that occurred with increased age. As the larvae grew older and assumed adult characteristics, fewer specimens were required for preservation.

During the study 89 larvae were preserved which ranged in age from one to 160 days. Observations on changes in body shape, fin development and coloration were made on each specimen. The following morphological measurements were made with a vernier stage micrometer attached to a dissecting microscope.

STANDARD LENGTH (SL) – length from the tip of the snout to the posterior end of the notochord or the hypural plate.

HEAD LENGTH (HL) – length from the tip of the snout to the rear edge of the gill cover.

MAXIMUM DEPTH (MAXD) – greatest body depth.

SNOUT-TO-DORSAL-FIN-ORIGIN LENGTH (SNTDO) – length from the tip of the snout to the anterior base of the dorsal fin.

SNOUT-TO-VENT LENGTH (SNTVT) – length from the tip of the snout to the anterior edge of the vent.

The snout-to-vent length as a percentage of standard length (SNTVT/SL x 100) was also calculated to determine relative proportional growth. Morphometric data on the larvae were punched on computer cards and analyzed on an IBM 260 computer to obtain mean data for each age group. Product moment correlation values (r) were also computed and plotted for various pairs of these data.

BEHAVIOR

Within a period of 7 to 10 days after the fishes were placed in the aquaria, one of the males assumed a dominant role and established a territory, that occupied approximately one-half of the total area of the tank and extended from the top to the bottom. Any individual that approached the territory was quickly confronted by the male and ultimately sent fleeing to the opposite end of the aquarium. Eventually, one of the females was allowed to enter the territory unmolested.

Once together, however, the male and female did not spawn immediately. The male seemed unattentive to the female and concentrated principally on maintaining his territorial perimeter. Meanwhile the female swam about the area in a seemingly nonchalant manner. Periodically, she proceeded to the bottom of the aquarium and scooped up a mouthful of sand. She held it in her mouth for an instant as if to test it, then spit it out and continued swimming about the

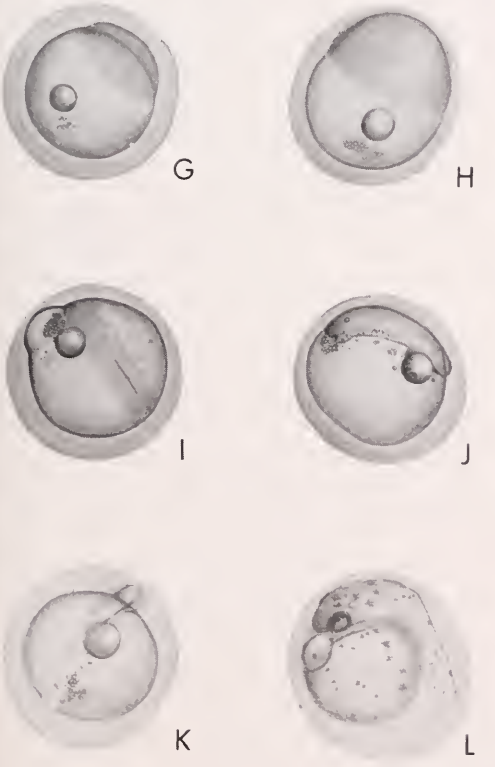

Figure 2. Developing eggs of *Cyprinodon variegatus*. G. Early neurula; H. Mid neurula; I. Late neurula; J. Six-somite stage; K. Ten-somite stage; L. Free-tail prolarva.

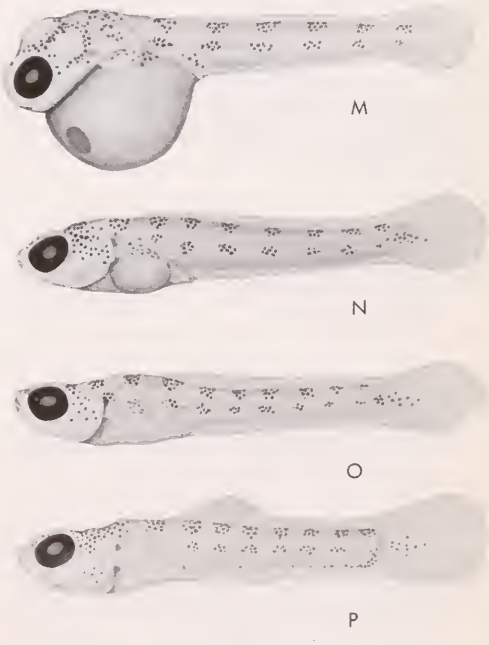

Figure 3. Larvae of *Cyprinodon variegatus*. M. Newly hatched prolarva (2.7 mm SL); N. 3-day old larva (3.5 mm SL); O. 8-day old larva (4.7 mm SL); P. 12-day old larva (5.6 mm SL).

territory. This behavior was repeated several times. After spitting out one of these mouthfuls, the female shoved her snout into the sand at the same spot and threw her head sideways, thereby raising a small cloud of sand particles up off the bottom.

Once he observed this behavior, the male's attentions changed immediately. He no longer seemed interested in defending his territory; instead he positioned himself by the side of the female and began to swim in unison with her. During this time, his body and fin coloration intensified tremendously. The dorsal part of his body and head turned almost black. On each shoulder there was an iridescent blue patch that measured approximately 3 to 5 mm wide and 8 to 12 mm long. The entire ventral surface turned a bright, brassy orange. The dorsal and caudal fins were moderate to bright yellow and each had a distinct black margin. The anal and pelvic fins were yellowish orange. The pectoral fins remained essentially clear. The color of the female changed very little during this time. The dorsal part of her body became slightly darker and her venter assumed a pale yellow while her pectoral, caudal and dorsal fins remained essentially clear. The black spot in her dorsal fin intensified only slightly.

After a brief period of swimming side by side, the pair settled to the bottom where the female had previously nosed the substrate. Suddenly, both fishes began to tremble violently. Simultaneously, they waved their caudal fins rapidly from side to side, creating a small cloud of sand particles in the water. At this time, the eggs and sperm must have been released and covered with sand, but the process occurred so rapidly that it was not actually observed. After the spawning act was completed, the male and female swam away from the area and any eggs that remained uncovered were quickly eaten by the other fishes that had congretaged around them.

Two activities that have been observed in the aquaria have not otherwise been reported in the literature. They appear, however, to be important aspects of the spawning ritual, because of the unfailing frequency with which they occurred. The first activity concerns the apparent control of the spawning time and place by the female. During each pairing, the male indicated no intent to spawn with the female until after she had "signaled" him by running her snout into the sand. Secondly, Newman (1907) indicated that the male almost forced the female to spawn by trapping her either in a corner of the aquarium or at the bottom. After he had captured her, he then "held the female just forward of her caudal fin, using chiefly his very strong dorsal fin." Neither the present authors nor Raney et al. (1953) ever observed the male to hold the female, even during the height of the spawning act.

Repeated observations of the substrate testing by the female followed by egg burial led to the conclusion that these two activi-

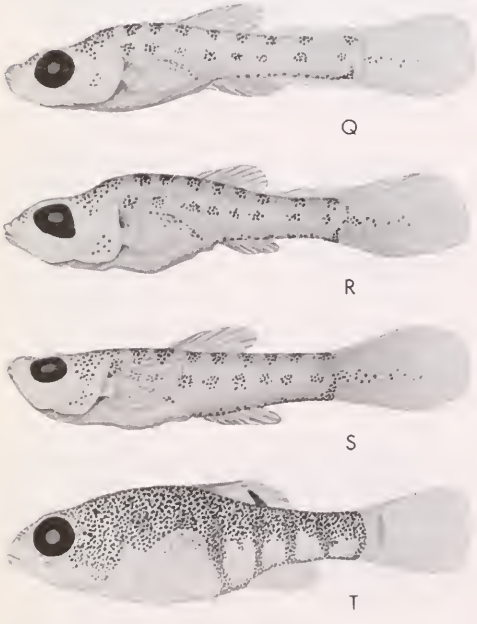

Figure 4. Larvae of *Cyprinodon variegatus*. Q. 16-day old larva (6.5 mm SL); R. 26-day old larva (7.5 mm SL); S. 40-day old larva (8.1 mm SL); T. 98-day old larva (14.4 mm SL).

ties were closely related and that they may represent an ecological adaptation to the heavy predation and/or other environmental conditions in the natural habitat of *Cyprinodon variegatus*. The same result was probably obtained by the nest construction followed by spawning that has been described by Nichols and Breder (1927) and Raney et al. (1953). Both of those reports described how a nest consisting of a clean shallow depression was constructed by a fish, usually a male, during which time he vigorously wiggled his venter against the substrate. The spawning act that followed invariably disturbed bottom sediments and debris which, upon settling, probably covered the eggs. The end result of this activity was that the eggs were out of sight and predation on them was probably reduced.

The spawning of *Cyprinodon variegatus* was observed on four different occasions during this study: 10:15 a.m. (21 April), 11:45 a.m. (1 May), 8:00 p.m. (15 April) and 9:45 p.m. (22 April). Raney et al. (1953) found that spawning activity of *C. variegatus* diminished in the late afternoon and ceased after dark. Nocturnal spawning of the fishes in the present study probably was due to the lengthy light period maintained by fluorescent light banks that masked the normal effects of dusk and darkness.

Spawning did not occur as a single act but consisted of a period of minutes during which a male and female spawned as many as six or seven times. Similar observations were made by Raney et al. (1953) in Florida.

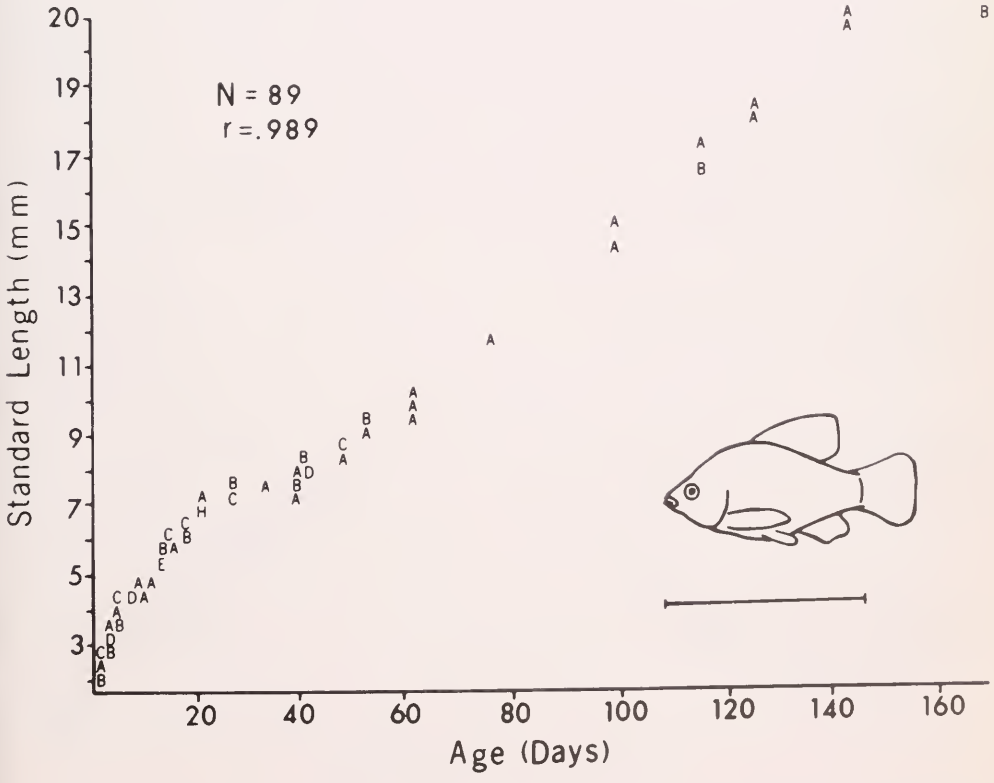

Figure 5. Growth of young *Cyprinodon variegatus* expressed as standard length. A= one observation, B= two observations, etc.

The number of eggs deposited during any one pairing could not be determined because of the rapidity with which the act occurred and their being covered. Moreover, it was not uncommon for the eggs of one spawning to be placed either close to or on top of the eggs from a previous one deposited during the same spawning period. Consequently, when the eggs were collected, they could not be assigned to one spawn or the other. Best estimates indicate that between 8 to 10 eggs were deposited per spawn.

EMBRYOLOGY

Two hundred and twenty-four eggs of *Cyprinodon variegatus* were collected and observed during the study. The newly laid eggs averaged 1.1 to 1.3 mm in diameter, were spherical, yellowish in color and demersal. Each egg contained a yolk that averaged 0.9 mm in diameter and each yolk contained one large, round oil droplet (0.2 mm average diameter) and numerous smaller ones of various sizes randomly distributed throughout it. The surface of each egg was covered with numerous tiny adhesive threads like those noted by Kuntz (1916). The threads caused eggs to stick to each other and any objects that they touched.

The following is a composite description of the various embryological stages that were observed during the study. The letter assigned to each stage corresponds to the drawings in Figures 1 and 2.

A. One-celled stage (45 minutes after fertilization)

Each egg has swelled slightly due to the infusion of water so that the average

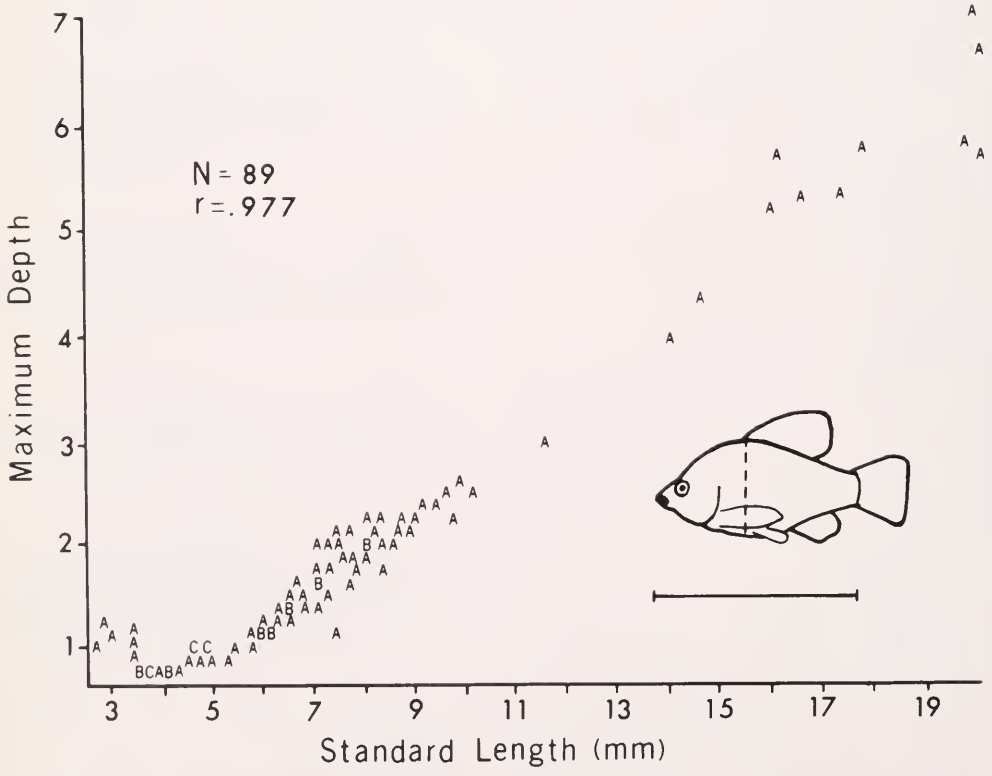

Figure 6. Proportions of young *Cyprinodon variegatus* expressed as maximum depth vs standard length. Legend as in Fig. 5.

diameter is 1.5 mm. A distinct perivitelline space is visible around each yolk. A prominent crescent-shaped structure, the blastodisk, is present on one side of the yolk.

B. Two-celled stage (75 minutes)

As a result of the first mitotic division, two blastomeres of equal size are formed. The chorion has become taut so that it is difficult to press downward on the egg without it being deflected to one side. The area immediately below the blastomeres now contains only a few oil droplets.

C. Four-celled state (2 hours)

The second cleavage occurs at right angles to the first and the resulting four blastomeres are equal in size and approximately one-quarter the dimensions of the previous two. Approximately one-fourth of the yolk below the blastomere is essentially clear of oil droplets.

D. Eight-celled stage (2½ to 3 hours)

The third cleavage occurs at right angles to the second and forms two rows with four blastomeres in each row. The cells appear to be slightly unequal in size. Approximately one-third of the yolk is free of oil droplets.

E. Early blastula (4 hours)

The early blastula stage is formed as the result of continuous asynchronous cell division at several planes. With each succeeding division, cell size has decreased.

F. Late blastula (6 to 7 hours)

Cell division has continued and a prominent berry-like structure called the morula is present on the side of the yolk.

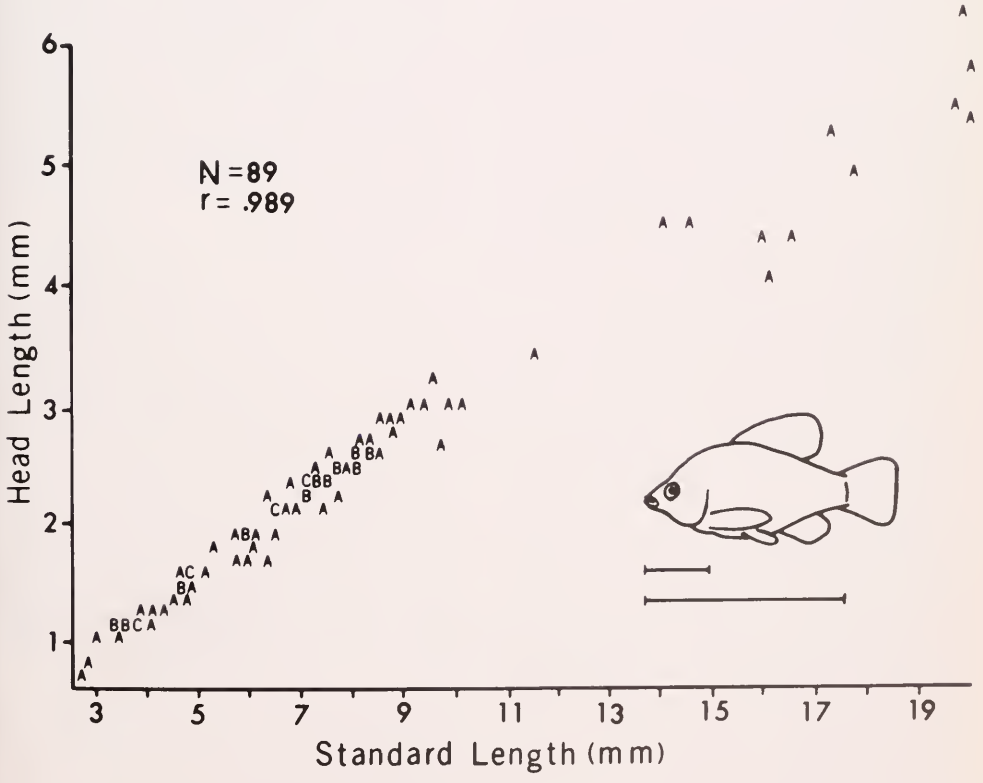

Figure 7. Proportions of young *Cyprinodon variegatus* expressed as head length vs standard length. Legend as in Fig. 5.

G. Early neurula (10 hours)

At the beginning of this stage, the morula becomes flattened on top and its base starts to spread out evenly over the surface of the yolk. Soon, the leading edge of this layer of cells (the germ ring) will thicken and slightly constrict the yolk.

H. Mid neurula (15 hours)

The blastoderm has migrated over approximately one-half of the yolk. The constriction of the yolk by the germ ring is more apparent.

I. Late neurula (22 to 23 hours)

The uncovered portion of the yolk is seen as a prominent bulge. The embryonic shield, which indicates the future longitudinal axis of the embryo, is visible as a thickened area on the blastoderm. The neural keel is present on the embryonic shield.

J. Six-somite stage (36 hours)

Six pairs of somites have developed at about the middle of the embryo. Its anterior end may be recognized by the optic placodes on either side of the head. There is a distinct dome on top of the head in the region of the midbrain. The large oil droplet is now positioned against the ventral side of the yolk opposite the developing embryo.

K. Ten-somite stage (48 to 50 hours)

The optic placodes are more circular around their edges and for the first time a faint outline of a pupil is present. The area over the midbrain has increased in size and there is also a slight bulge over the area of the hind brain. The first melanophores have developed on the dorsolateral portions of the yolk and each adjacent side of the body. The yolk has decreased slightly in size. Immediately anterior to it is a small cavity that contains the structure that will become the heart. The heart is not beating at this time. The notochord is visible as a rod that extends from the rear edge of the brain posteriorly to the end of the body.

L. Free-tail prolarva (90 hours)

The ventral edge of the posterior end of the body has completely separated from the yolk, and this forms the basis for the name of this stage. The tail has oriented to one side of the body because of the occasional wriggling of the prolarva inside the egg. The eyes appear to be fully formed and the iris of each is turning black. A small pectoral fin bud is present on either side of the body immediately posterior to the head and dorsal to the yolk. Melanophores are present on the snout and the dorsal and lateral sides of the body. Three or four concentrations of melanophores on the back form dorsal saddles. The heart is pumping at 104 to 106 beats per minute. The blood is light pink in color and the circulatory pathway throughout the head and body is visible. Twenty to 22 somites are present in the posterior three-fourths of the body, many of which occur as myomeres of muscle. A continuous fin fold is present; it arises on the dorsal midline above the yolk, extends posteriorly around the tail and anteriorly on the ventral midline to the vent. The first indications of two or three caudal fin rays are present in the fin fold.

THE HATCHING PROCESS

The earliest time at which hatching occurred was between 120-125 hours after fertilization, the temperature having been 23°C ±1°. The majority of the prolarvae had hatched by 150 hours but a few required as long as 160 to 170 hours.

Prior to hatching, the movements of each prolarva became more frequent and violent inside the egg. During one of these periods, the chorion ripped and this freed the posterior end of the fish. After a brief rest, the prolarva vigorously shook its head from side to side and eventually managed to free itself from the egg.

For the first few hours, the prolarvae remained motionless, lying on their sides on the bottom. Periodically, one or two individuals darted ahead for a short distance along the bottom or swam upward in the

water column in a short burst of speed. As quickly as they started, however, they stopped and drifted back to the bottom.

DESCRIPTION OF THE PROLARVA

The newly hatched prolarva of *Cyprinodon variegatus* was tear-drop in shape except for the large round yolk on its ventral side (Figure 3,M). Total length averages 3.0 mm and standard length 2.7 mm (Table 1). The eyes were black with a gray iris. Kuntz (1916) noted that the head of *Cyprinodon variegatus* was not deflected; however, it was deflected on all of the newly hatched prolarvae that were observed in the present study. It is not certain if the references to the non-deflected head by Lippson and Moran (1974) and Scotton et al. (1973) were based on Kuntz (1916) or on original observation. A large bump occurred on top of the head over the enlarging brain. A small, incompletely formed mouth was visible in a terminal position on the snout. The rear edges of the opercles were free and moved as the prolarva breathed.

The body of the prolarva was translucent pale yellow and the dorsal and lateral portions of it and the head were covered with randomly distributed melanophores. Seven or eight irregular saddles of melanophore concentrations appeared on the back. The total number of myomeres in the body varied from 23 to 26. Postanal myomeres ranged from 16 to 19 but averaged 17 or 18. Inside the yolk and located along its anterio-ventral wall was a small but distinct oil

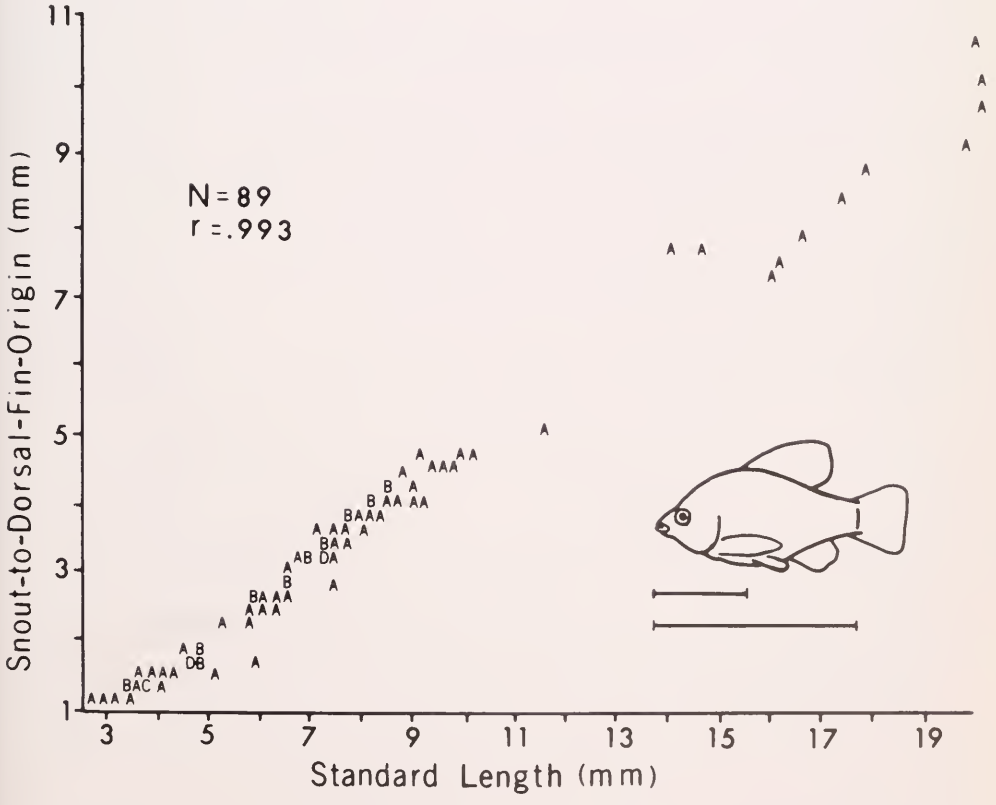

Figure 8. Proportions of young *Cyprinodon variegatus* expressed as snout-to-dorsal-fin-origin length vs standard length. Legend as in Fig. 5.

droplet. The heart was easily seen inside the pericardial cavity which was located immediately anterior to the yolk in the area of the isthmus. The heart beat averaged 124-125 beats per minute. The blood was light pink, the erythrocytes were distinguishable and their pathway throughout most of the body was easily observed.

A continuous finfold was present on the dorsal midline, slightly behind the head. It extended around the posterior end of the body and continued anteriorly on the ventral midline to the vent. Six or seven caudal fin ray primordia were present but no dorsal or anal primordia could be seen. A small pectoral fin bud that contained no rays was present on either side of the body immediately posterior to the opercle. No pelvic fin buds were observed on the newly hatched prolarvae.

LARVAL DEVELOPMENT

Growth of *Cyprinodon variegatus* larvae was rapid. Age vs standard length is presented in Table 1 and Fig. 5; various morphological measurements in relation to standard length are presented in Table 1 and Figs. 6-9. Figures 3 and 4 depict significant morphological stages during larval development.

YOLK: Shortly after hatching, the yolk began to decrease noticeably in size. On day 3 (Figure 3,N), only a small portion was left and the oil droplet was not discernible. By day 8 (Figure 3,O), the yolk had completely disappeared.

FINS: Dorsal fin ray primordia were first apparent on 9- and 10-day old larvae. Twelve-day old larvae (Figure 3,P) possessed

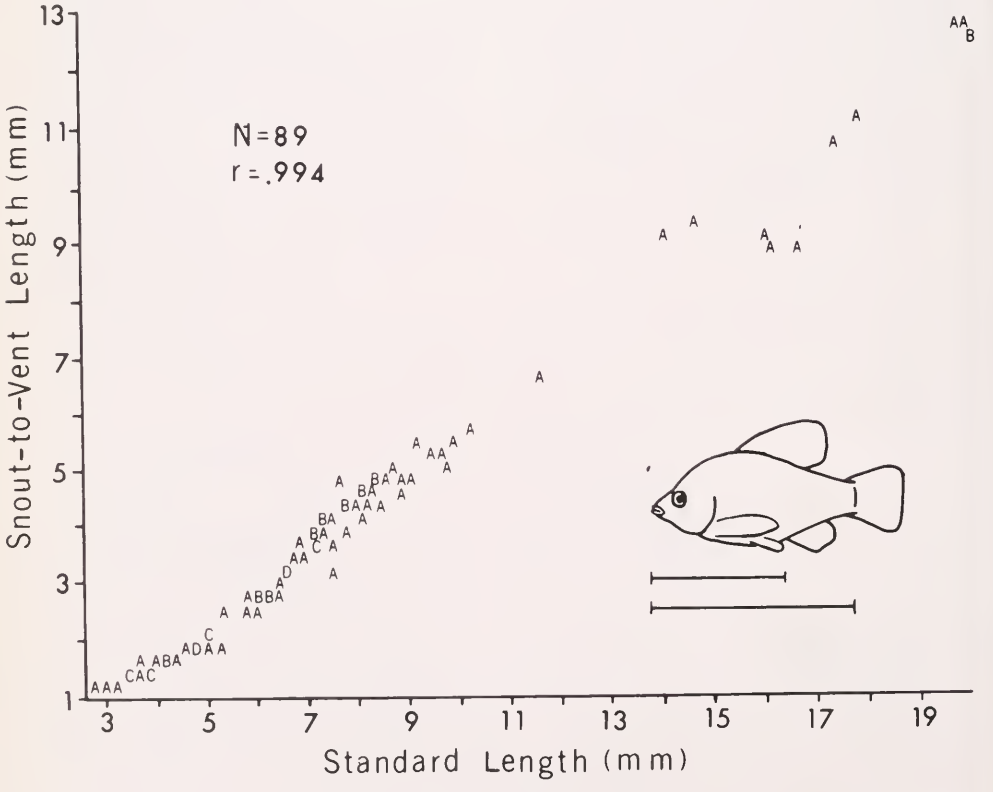

Figure 9. Proportions of young *Cyprinodon variegatus* expressed as snout-to-vent length vs standard length. Legend as in Fig. 5.

Table 1. MEAN DATA FOR MORPHOMETRIC MEASUREMENTS MADE ON 139 AQUARIUM-RAISED SPECIMENS OF CYPRINODON VARIEGATUS: N = Number; SL = Standard length; HL = Head length; SNTL = Snout length; EL - Maximum eye width; SNTDO = Snout to dorsal fin origin length; SNTVT = Snout to vent length; MAXD = Maximum depth; and SNTVT/SL x 100 = Snout to vent length divided by standard length x 100.

Age	N	SL	HL	SNTL	EL	SNTDO	SNTVT	MAXD	SNTVT/SL x 100
1*	53	2.7	0.6	0.1	0.2	1.1	1.3	1.1	47.0
2	3	3.3	0.9	0.1	0.3	1.3	1.5	1.0	45.0
3	7	3.6	1.0	0.2	0.3	1.4	1.7	0.8	45.6
4	2	4.0	1.1	0.2	0.4	1.5	1.8	0.7	43.8
5	4	4.6	1.3	0.2	0.5	1.8	2.0	1.0	44.4
8	4	4.7	1.4	0.3	0.5	1.9	2.9	1.0	46.1
9	2	4.9	1.4	0.3	0.5	1.7	2.1	1.0	41.8
10	1	5.2	1.7	0.3	0.6	2.3	2.6	1.0	50.0
13	7	5.8	1.7	0.4	0.6	2.5	3.0	1.1	49.6
15	4	6.4	2.0	0.4	0.7	2.8	3.2	1.4	50.4
18	5	6.6	2.1	0.5	0.7	3.2	3.6	1.5	53.9
21	9	7.1	2.3	0.4	0.8	3.4	4.0	1.7	55.5
26	5	7.5	2.3	0.5	0.8	3.8	4.3	2.0	57.0
32	1	7.8	2.4	0.6	0.8	3.9	4.5	1.8	57.7
38	4	7.8	2.5	0.6	0.9	3.9	4.7	2.0	59.5
40	6	8.2	2.6	0.6	0.9	4.2	4.8	2.0	58.2
47	4	8.8	2.9	0.7	1.0	4.3	5.0	2.2	56.6
51	3	9.4	3.0	0.7	1.1	4.7	5.4	2.4	57.3
60	3	9.8	3.1	0.7	1.2	4.8	5.7	2.6	57.9
75	1	11.5	3.5	0.9	1.3	5.2	6.9	3.1	60.0
98	2	14.3	4.8	1.2	1.5	8.0	9.5	4.3	66.1
115	3	16.2	4.5	1.1	1.5	7.8	9.2	5.5	56.4
125	2	17.6	5.5	1.4	2.0	9.0	11.2	5.8	63.5
143	2	20.0	5.9	1.6	1.8	9.9	12.9	5.9	64.5
170	2	20.1	6.6	1.6	2.2	10.9	12.9	7.1	64.1

*Day 1 measurements were made on 50 live and 3 preserved individuals.

about the same numbers of dorsal and anal fin primordia. On day 16 (Figure 4,Q), segmentation was visible at the bases of several of the dorsal and anal rays which had increased in length. The ventral fin fold and part of the dorsal fin fold had disappeared by day 26 (Figure 4,R). At 40 days after hatching (Figure 4,S), all remnants of the fin fold had disappeared and for the first time, tiny pelvic fin buds were present on either side of the mid-ventral line. Several rays were present in each of the pectoral fin buds. At the juvenile stage (Figure 4,T) all fins were completely developed.

THE HEAD. Lippson and Moran (1974) indicated that the mouth on larval *Cyprinodon variegatus* was superior. In our specimens, however, it occupied a more or less terminal position. As the yolk disappeared, the head assumed a more horizontal

position. The eyes were large, even in newly hatched prolarvae, their diameter averaging one-third the head length. An otolith was present in a position immediately posterior to each eye. The dorsal and lateral sides of the head contained scattered melanophores, the number of which increased with age so that the head of a 98-day old juvenile (Figure 4,T) was completely covered except for the ventral surface.

THE BODY: The body of the youngest larva was fairly elongated and compressed. Within three to four weeks after hatching, it began to assume the more diamond-shaped appearance characteristic of adults. The notochord was easily visible as a rod extending almost the entire length of the body, but it gradually became indistinguishable as the body became more opaque and the vertebral column developed at approximately days 20 and 24. Although the number of body melanophores increased, their distribution remained unchanged until about 60 days when they began to appear over most of the back and sides. By 98 days (Figure 4,T), they covered most of the body except the ventral region anterior to the vent and several irregularly shaped patches on either side above the anal fin and on the caudal penducle.

GROWTH: Figure 5 indicates the direct relationship between age and standard length ($r = .989$) in the young *Cyprinodon variegatus*. The decrease in maximum depth in Figure 6 is due to yolk absorption. Shortly thereafter, the maximum depth began to increase proportionately with standard length ($r = .977$) as the larvae began to actively feed on the *Artemia* nauplii. The small, abrupt increase in head length at 3 to 3.5 mm standard length in Figure 7 is due to yolk absorption and the subsequent upturn of the head, especially the snout, to assume a more horizontal position. The relationship between snout-to-dorsal-fin-origin and standard length (Figure 8) is highly correlated, with an r value of .993. Snout-to-vent length versus standard length are also highly correlated ($r = .994$) in Figure 9.

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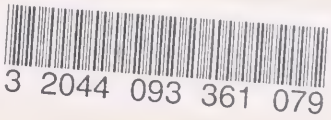
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